TAXONOMIC REVISION OF THE MOSS GENUS *LEPIDOPILIDIUM* (PILOTRICHACEAE)[1]

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Abstract

Lepidopilidium (Müll. Hal.) Broth. (Pilotrichaceae) consists of mainly epiphytic and epiphyllous, pleurocarpous mosses distributed in the tropical, subtropical, and south temperate regions of Central America, South America, Africa, southern India, and Sri Lanka. The genus is characterized by a moderately to strongly complanate habit; the presence of a moderately to well-developed stem hyalodermis; dimorphic dorsal, ventral, and lateral leaves; prominent double costae; smooth, hexagonal, rhomboidal, or fusiform leaf cells; smooth or papillose setae; collenchymatous exothecial cells; 2-celled stomata; massive annuli; a hookeriaceous-type peristome; and sparsely pilose or glabrous mitrate calyptrae. Six species are taxonomically accepted: *L. brevisetum* (Hampe) Broth., *L. devexum* (Mitt.) Broth., *L. divaricatum* (Dozy & Molk.) Broth., *L. furcatum* (Thwaites & Mitt.) Broth., *L. isleanum* (Besch.) Broth., and *L. nitens* (Hornsch.) Broth., with 19 names newly synonymized. *Lepidopilum chenagonii* Renauld & Cardot is transferred to *Thamniopsis* (Mitt.) M. Fleisch., as *T. chenagonii* (Renauld & Cardot) J. J. Atwood. *Lepidopilidium crispifolium* W. R. Buck & Wigginton and *Hookeria pallidifolia* Mitt. are placed in *Hookeriopsis* (Besch.) A. Jaeger s. str., as *H. crispifolia* (W. R. Buck & Wigginton) J. J. Atwood and *H. pallidifolia* (Mitt.) Geh. & Herzog, respectively. *Lepidopilum plebejum* (Müll. Hal.) Sehnem is treated as a new synonym of *Lepidopilum pallidonitens* (Müll. Hal.) Paris. Typification is designated for the unranked Lamprophyllum group of *Hookeria* Sm. by *Hookeria nitens* Hornsch. [≡ *Lepidopilidium nitens*] and for *Lepidopilum* sect. *Plagiotheciella* Besch. by *Lepidopilum isleanum* Besch. [≡ *Lepidopilidium isleanum*]. Typifications are designated for *Crossomitrium portoricense* Müll. Hal. [≡ *Lepidopilidium portoricense* (Müll. Hal.) H. A. Crum & Steere; = *L. nitens*], *Hookeria aureopurpurea* Geh. & Hampe [≡ *Lepidopilidium aureopurpureum* (Geh. & Hampe) Broth.; = *L. nitens*], *Hookeria aureopurpurea* Müll. Hal. [≡ *Lepidopilidium lamprophylloides* (Paris) Broth.; = *L. brevisetum*], *Hookeria breviseta* Hampe [≡ *Lepidopilidium brevisetum*], *Hookeria divaricata* Dozy & Molk. [≡ *Lepidopilidium divaricatum*], *Hookeria entodontella* Müll. Hal. ex Broth. [≡ *Lepidopilidium entodontella* (Müll. Hal. ex Broth.) Broth.; = *L. nitens*], *Hookeria gracilifrons* Müll. Hal. [≡ *Lepidopilidium gracilifrons* (Müll. Hal.) Broth.; = *L. nitens*], *Hookeria longicuspis* Müll. Hal. [≡ *Lepidopilidium longicuspis* (Müll. Hal.) Broth.; = *L. nitens*], *Hookeria nitens* Hornsch. [≡ *Lepidopilidium nitens*], *Hookeria subnitens* Geh. & Hampe [≡ *Lepidopilidium subnitens* (Geh. & Hampe) Broth.; = *L. nitens*], *Hookeria subnitens* Geh. & Hampe var. *latior* Geh. & Hampe [= *Lepidopilidium nitens*], *Hookeria tenuiseta* Müll. Hal. [≡ *Lepidopilidium tenuisetum* (Müll. Hal.) Broth.; = *L. nitens*], *Hookeria wainioi* Broth. [≡ *Lepidopilidium wainioi* (Broth.) Broth.; = *L. nitens*], *Lepidopilum corbieri* Renauld & Cardot [≡ *Lepidopilidium corbieri* (Renauld & Cardot) Cardot; = *L. divaricatum*], *Lepidopilum devexum* Mitt. [≡ *Lepidopilidium devexum*], *Lepidopilum flexuosum* Besch. [≡ *Lepidopilidium flexuosum* (Besch.) Broth. ex Paris; = *L. isleanum*], *Lepidopilum fruticola* Müll. Hal. [≡ *Lepidopilidium fruticola* (Müll. Hal.) Broth.; = *L. brevisetum*], *Lepidopilum furcatum* Thwaites & Mitt. [≡ *Lepidopilidium furcatum*], *Lepidopilum hanningtonii* Mitt. [≡ *Lepidopilidium hanningtonii* (Mitt.) Broth.; = *L. furcatum*], *Lepidopilum isleanum* [≡ *Lepidopilidium isleanum*], *Lepidopilum laevisetum* Hampe [≡ *Lepidopilidium laevisetum* (Hampe) Broth.; = *L. nitens*], *Lepidopilum subdevexum* Broth. [≡ *Lepidopilidium subdevexum* (Broth.) Broth.; = *L. devexum*], *Lepidopilum subdivaricatum* Renauld & Cardot [≡ *Lepidopilidium subdivaricatum* (Renauld & Cardot) Broth.; = *L. divaricatum*], *Lepidopilum subrevolutum* Renauld & Cardot [≡ *Lepidopilidium subrevolutum* (Renauld & Cardot) Cardot; = *L. isleanum*], *Lepidopilidium attenuatum* Thér. [= *L. furcatum*], *Lepidopilidium brevisetum* (Hampe) Broth. var. *purpurascens* Broth. [= *L. brevisetum*], *Lepidopilidium parvulum* Schimp. ex Cardot [= *L. isleanum*], *Lepidopilidium theriotii* Naveau [= *L. furcatum*], *Lepidopilidium subdevexum* Broth. (Broth.) var. *intermedium* P. de la Varde [= *L. devexum*], and *Lepidopilidium synoicum* Herzog [= *L. divaricatum*].

Key words: Africa, Central America, *Hookeriopsis*, India, *Lepidopilidium*, *Lepidopilum*, Pilotrichaceae, South America, Sri Lanka, *Thamniopsis*.

Within the Hookeriales there are several generic pairs that are gametophytically similar to each other but have dissimilar sporophytes. Such pairings include *Crosbya* Vitt and *Daltonia* Hook. & Taylor, *Distichophyllum* Dozy & Molk. and *Leskeodon* Broth., *Stenodesmus* (Mitt.) A. Jaeger and *Stenodictyon* (Mitt.) A. Jaeger, and *Lepidopilidium* (Müll. Hal.) Broth. and *Lepidopilum* (Brid.) Brid. Gametophytic similarities between *Lepidopilidium* and *Lepidopilum* species are particularly seen in the scabrisetum group based on *Lepidopilum scabrisetum* (Schwägr.) Steere. Of the 40 validly published names in *Lepidopilidium*, 18 were

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at one time placed in *Lepidopilum*. *Lepidopilidium* and the *Lepidopilum* species in the scabrisetum group are characterized by a moderately to strongly complanate habit; the presence of a stem hyalodermis; 2-celled axillary hairs; rhizoids clustered on the ventral surface of the stem or abaxial to the leaf insertion; dimorphic dorsal, ventral, and lateral leaves; prominent double costae; and smooth, hexagonal, rhomboidal, or fusiform leaf cells. Despite these gametophytic similarities, the sporophytes of the two genera are mostly at extremes with each other. *Lepidopilidium* has smooth to papillose setae and sparsely pilose or glabrous calyptrae, whereas *Lepidopilum* has papillose to scabrous setae and pilose to rarely glabrous calyptrae. However, the best means of distinguishing *Lepidopilidium* from *Lepidopilum* is by their different peristome types. *Lepidopilidium* has a hookeriaceous-type peristome that is composed of dark red, narrowly triangular exostome teeth that are furrowed, thickened, proximally cross-striate, and distally papillose on the outer (dorsal) surface. The endostome consists of a high basal membrane and finely papillose segments. By contrast, *Lepidopilum* has a daltoniaceous-type peristome that consists of pale, linear to very narrowly triangular exostome teeth that lack median furrows and are thin and papillose on the outer (dorsal) surface throughout. The endostome is composed of papillose segments above a high or low basal membrane. These two contrasting peristome types further differ in their hygroscopic movement. The exostome teeth in the hookeriaceous peristome type of *Lepidopilidium* are incurved when hydrated and reflexed when dehydrated, whereas in the daltoniaceous peristome type of *Lepidopilum* they are incurved when dehydrated and reflexed when hydrated (Whittemore & Allen, 1989).

The oldest known name in *Lepidopilidium* (Pilotrichaceae) is *Hookeria nitens* Hornsch. (Hornschuch, 1840). This species and *H. glaziovii* Hampe [= *Thamniopsis langsdorffii* (Hook.) W. R. Buck] were considered by Hampe (1874) within the unranked Lamprophyllum group of *Hookeria* Sm., which included species that were superficially similar to *Lepidopilum* but differed in having smooth setae ornamentation and a hookeriaceous-type peristome. Additional species were subsequently added to the group by Hampe (1878), Geheeb and Hampe (1881), and Müller (1900), who in addition established another group in *Hookeria*, parenthetically cited as "Lepidopilidium." Müller's intentions for the Lepidopilidium group are unclear since he did not formally designate a rank. In the same publication (1900: 235–236), however, he cites "Pseudepheme-rum" in a similar manner within the new species *Ephemerum perexiguum* Müll. Hal. His intention of designating a new section within *Ephemerum* Hampe is found in the diagnoses. Following the provision of Article 37.5 of the International Code of Botanical Nomenclature (McNeill et al., 2012), all parenthetically cited names in this paper should be treated similarly, in this case as sections. *Hookeria* sect. *Lepidopilidium* Müll. Hal. was noted as superficially similar to *Lepidopilum*, but it differed in having a hookeriaceous- versus daltoniaceous-type peristome. Three species newly described by Müller (1900) were placed in this section: *Hookeria* (*Lepidopilidium*) *tenuiseta* Müll. Hal., *Hookeria* (*Lepidopilidium*) *longicuspis* Müll. Hal., and *Hookeria* (*Lepidopilidium*) *rupestris* Müll. Hal., the first of which was later designated by Welch (1969) as the lectotype of *Lepidopilidium*.

Brotherus (1907) elevated *Hookeria* sect. *Lepidopilidium* to generic rank and significantly expanded it by including species from the unranked Lamprophyllum group of *Hookeria* and *Lepidopilum*. The genus then encompassed 24 species that were separated by variation in lateral leaves, sexuality, setae length and ornamentation, capsule shape and orientation, and spore size. Regional treatments of *Lepidopilidium*, as well as revisions of related genera, have since resulted in the description of seven more taxa (Renauld & Cardot, 1915; Herzog, 1916; Brotherus, 1924; Thériot, 1930; Potier de la Varde, 1939; Dixon & Thériot, 1942; Wigginton & Buck, 2013), the transfer of 10 taxa to *Lepidopilidium* (Paris, 1909; Renauld & Cardot, 1915; Crum & Steere, 1956; Sehnem, 1979; Buck & Ireland, 1989; Vaz-Imbassahy & Costa, 2009), one transfer out of *Lepidopilidium* to *Lepidopilum* (Sehnem, 1979; Vaz & Costa, 2006; Vaz-Imbassahy & Costa, 2008), and the placement of eight names into synonymy within *Lepidopilidium* (Brotherus, 1924; Buck, 1998; Churchill et al., 2000; Vaz & Costa, 2006; Vaz-Imbassahy & Costa, 2008; Allen, 2010). Among the now 40 validly published names in *Lepidopilidium*, 29 species are currently recognized, along with two varieties.

Lepidopilidium has never been the subject of a worldwide revision, and the delimitation of taxa as well as their distributions are not sufficiently resolved (Buck, 1998; Gradstein et al., 2001; Allen, 2010; Costa et al., 2011; Wigginton & Buck, 2013). Additionally, *Lepidopilidium* is reported to be paraphyletic in its present circumscription (Buck et al., 2005), with one *Lepidopilidium* accession nested within a clade with *Lepidopilum* and *Stenodictyon wrightii* (Sull. & Lesq.) Crosby, while a second is

nested in a clade with *Thamniopsis* (Mitt.) M. Fleisch. *Lepidopilidium*, as circumscribed here, is considered to be monophyletic. In the phylogeny by Buck et al. (2005), the alignment of the *Lepidopilidium laevisetum* accession (*Schäfer-Verwimp 9237*, NY) with *Thamniopsis* is in agreement with their similar morphology. All members of this clade share a hookeriaceous-type peristome. On the other hand, the alignment of the *Lepidopilidium portoricense* accession (*Buck 37825*, NY) with *Lepidopilum* and *Stenodictyon* couples hookeriaceous and daltoniaceous peristome types together in a clade. A re-examination of the *Lepidopilidium portoricense* specimen found it to be a misdetermined specimen of *Lepidopilum scabrisetum*. As previously noted, sporophyte characters provide the best means for separating *Lepidopilidium* from *Lepidopilum*, although sporophytes are lacking in this specimen. Utilizing gametophyte characters is much more difficult as it requires familiarity with the species in *Lepidopilidium* as well as the scabrisetum group of *Lepidopilum*. Welch (1976) observed that the median leaf cells in *Lepidopilidium* are usually wider than those of *Lepidopilum* and have a length:width ratio of 10:1. Conversely, the median leaf cells of *Lepidopilum* are usually longer and narrower, with a ratio of 22:1. In addition, the lateral leaves of *Lepidopilum scabrisetum* tend to be more sigmoid in shape than those of *Lepidopilidium*. Allen (2010) noted that *Lepidopilidium* sometimes has narrowly recurved upper leaf margins, whereas the upper leaf margins of species in the scabrisetum group in *Lepidopilum* are plane. Lastly, most Neotropical *Lepidopilidium* are dioicous, whereas most Neotropical specimens of *Lepidopilum scabrisetum* are autoicous, although dioicous forms exist (Churchill, 1988). By replacing the *Lepidopilidium portoricense* accession with *Lepidopilum scabrisetum*, a more morphologically related clade is obtained, now composed of two *Lepidopilum scabrisetum* accessions, *L. polytrichoides* (Hedw.) Brid. and *Stenodictyon wrightii*. Since *S. wrightii* has a hookeriaceous-type peristome, it remains an oddity within this otherwise daltoniaceous-type peristome clade. Also peculiar is that another *Stenodictyon* species included in the phylogeny appears to be unrelated. A possible explanation for this incongruity is that the *S. wrightii* accession may also be based on a misdetermination. The corresponding specimen was not re-examined in this study. However, according to Allen (2010), the former concept of *S. wrightii*, presented in a review of the genus (Allen et al., 1986), confuses non-sporophyte material with several other species. Among these species are *Lepidopilum longifolium* Hampe and *Stenodesmus tenuicuspis* (Mitt.) A. Jaeger, both of which have a daltoniaceous-type peristome.

Lepidopilidium is currently recognized to contain the following six species: *L. brevisetum* (Hampe) Broth., *L. devexum* (Mitt.) Broth., *L. divaricatum* (Dozy & Molk.) Broth., *L. furcatum* (Thwaites & Mitt.) Broth., *L. isleanum* (Besch.) Broth., and *L. nitens* (Hornsch.) Broth. In addition, 19 names are newly synonymized, five names are transferred to other genera, and five names remain insufficiently known because their type specimens could not be located.

Materials and Methods

This taxonomic revision is based on approximately 40 type and 600 non-typic specimens from 14 herbaria (B, BM, BR, FH, G, H, JE, L, M, MO, NY, PC, S, US). Although all specimens were examined and annotated using standard practices, only those with complete and adequate material for sampling were used in the descriptions and illustrations. All measurements were made using rehydrated material mounted in Hoyer's solution (Anderson, 1954). Leaves selected for measurements were removed from the middle of the stem. Lamina length was measured from the leaf tip to the base, and lamina width was measured at the widest point. Cellular measurements include the cell wall. Measurements of the capsule urn exclude the operculum. The peristome was measured from the tip of the exostome teeth or endostome segment to the capsule mouth. Spore mounts were made from mature capsules, in which the operculum was removed after rehydration. The terminology for bryological characters follows Magill (1990). The taxonomic nomenclature includes the complete type citation from the original protologue. Species are defined using a taxonomic species concept that delimits groups according to their overall similarities. Distribution and habitat data are based on herbarium specimen labels. All specimens examined in this study are cited, although some details regarding their locality have been shortened or omitted for brevity.

Taxonomic Treatment

Lepidopilidium (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 942. 1907. *Hookeria* Sm. sect. *Lepidopilidium* Müll. Hal., Hedwigia 39: 272. 1900. TYPE: *Hookeria tenuiseta* Müll. Hal. (lectotype, designated by Welch, 1969: 123).

Hookeria [unranked] *Lamprophyllum* Hampe, in Warm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn ser.

3, 6: 158. 1874. TYPE: *Hookeria nitens* Hornsch. (lectotype, designated here).

Lepidopilum sect. *Plagiotheciella* Besch., Ann. Sci. Nat. Bot., sér. 6, 10: 279. 1880. TYPE: *Lepidopilum isleanum* Besch. (lectotype, designated here).

Plants dull or glossy, yellow, golden, green, or brown, often tinted red or purple, in lax to dense mats, occasionally tufts; stems prostrate, to 7 cm, spreading or erect, unbranched or irregularly branched with numerous short branches, moderately to strongly complanate-foliate; in cross-section with a moderately to well-developed hyalodermis, 2 to 4 rows of small, yellowish brown, thick-walled, subepidermal cells and large, hyaline, thin-walled, cortical cells; central strand absent; paraphyllia and pseudoparaphyllia absent; axillary hairs 2-celled, basal cell hyaline or brownish hyaline, short-rectangular, upper cell hyaline, oblong; rhizoids reddish brown, smooth, irregularly branched, arising from clusters of initials on ventral surface of primary stems, abaxial to leaf insertion and at base of costae. Leaves arranged in 8 rows, evenly or densely spaced, weakly to strongly dimorphic, flat or weakly concave, shriveled, contorted, or flexuous, appressed, erect, erect-spreading, or wide-spreading when dry. Dorsal and ventral leaves symmetric or weakly asymmetric, elliptical, ovate, oblong-ovate, or oblong-lanceolate, abruptly acute to short-acuminate. Lateral leaves weakly symmetric to strongly asymmetric, elliptical, ovate, oblong-ovate, oblong-lanceolate, or lanceolate, straight or falcate, abruptly acute, broadly to narrowly, short- or long-acuminate, sometimes slenderly acuminate; margins serrulate, serrate, or sharply serrate above, a few teeth occasionally inflated or bifurcate, serrulate to entire below, plane or more often narrowly recurved, sometimes broadly infolded on one side at base, straight to rounded to the insertion, elimbate or with 1 or 2 rows of elongate, narrow cells; costae double, prominently extending to about midleaf, parallel or diverging throughout, uneven, smooth or weakly serrate-toothed at back, not projecting or strongly projecting at tips; laminal cells smooth, thin- or thick-walled, sometimes porose, apical and median cells hexagonal, rhomboidal, or fusiform, becoming oblong-rectangular below; alar cells not differentiated; a single row of rounded, bulging cells along leaf insertion. Asexual reproduction by hyaline or reddish brown, smooth, filamentous, multicellular, uniseriate gemmae, arising from clusters of initials abaxial to leaf insertion and at base of costae. Plants autoicous, synoicous, or dioicous. Setae short to elongate, yellow to red, smooth throughout, smooth below and lightly or densely papillose above, or papillose throughout. Capsules red-brown, erect, suberect, or inclined, obloid to obloid-cylindrical, neck well-developed; exothecial cells subrectangular, collenchymatous; stomata on neck, 2-celled, phaneroporic; opercula short to long conic-rostrate; annuli of 3 to 10 rows of fragmenting, quadrate cells, persistent on opercula or capsule mouth; peristome diplolepideous; exostome teeth narrowly triangular, median furrows present, outer (dorsal) surface dark red, proximally cross-striate, distally papillose, inner (ventral) surface yellow, lightly papillose; endostome segments about as long as exostome, pale to yellow, lightly papillose throughout, concave-keeled, narrowly perforate, cilia absent. Spores spherical, yellow, finely papillose. Calyptrae mitrate, pale to yellow or red, smooth to weakly scabrous at tip, lacinate at base, sparsely pilose or glabrous.

Nomenclatural notes. Müller (1900) simultaneously described the species *Hookeria tenuiseta*, *H. longicuspis*, and *H. rupestris* in *Hookeria* sect. *Lepidopilidium*. Although all three species share equal priority, Welch (1969) selected *H. tenuiseta* as the lectotype of the genus without further justification. Her seemingly mechanical method of designating generic types with the first published name follows a pattern used for type selection by her in other genera, e.g., *Amblytropis* (Mitt.) Broth., *Hypnella* (Müll. Hal.) A. Jaeger, and *Hookeriopsis* (Besch.) A. Jaeger. Crosby et al. (1985) found reason to supersede the mechanically selected lectotype in *Hypnella*. In *Lepidopilidium*, however, Welch's type selection is retained due to the short generic description that follows *H. tenuiseta*.

Hampe's (1874) Lamprophyllum group in *Hookeria* was established for *H. nitens* [≡ *Lepidopilidium nitens*] and *H. glaziovii* [= *Thamniopsis langsdorffii*]. *Hookeria nitens* is designated herein as the type of this unranked group.

Lepidopilum sect. *Plagiotheciella* was established by Bescherelle (1880) to include *L. isleanum* and *L. cespitosum* Besch. The type of *L. cespitosum* could not be located, although the taxon appears to better affine within *Thamniopsis*. *Lepidopilum isleanum* is designated herein as the type of this section.

Discussion. *Lepidopilidium* forms mostly lax to dense, moderately to strongly complanate-foliate mats of spreading, prostrate to erect stems, up to 7 cm in length. Occasionally, as in *L. furcatum*, plants sometimes form tufts of erect stems. In cross-section, the stems have a moderately to well-developed hyalodermis; two to four rows of small, yellowish brown, thick-walled subepidermal cells; and large, hyaline, thin-walled, cortical cells. Rhizoid initials are located along the ventral surface of the stem or

clustered abaxial to the leaf insertion and at the base of the costae. The clusters of initials may produce rhizoids, gemmae, or both. The rhizoids are reddish brown, smooth, and irregularly branched. The gemmae are filamentous, hyaline or reddish brown, smooth, uniseriate, and multicellular, and occur abundantly in *L. brevisetum*, *L. furcatum*, *L. isleanum*, and *L. nitens*. Other features of *Lepidopilidium* include 2-celled axillary hairs and the lack of paraphyllia and pseudoparaphyllia. Foliose, short-triangular primordial leaves clustered around the branch buds can be confused for pseudoparaphyllia.

Due to the complanate-foliate habit of the stems, the dorsal and ventral leaves differ from lateral leaves in size, symmetry, and shape. The dorsal and ventral leaves are typically appressed or erect; symmetric or weakly asymmetric; ovate, oblong-ovate, or oblong-lanceolate; and have acute to shortly acuminate apices. Much of the described variation in *Lepidopilidium* is based on lateral leaf characters. The lateral leaves are erect, erect-spreading, or wide-spreading; weakly symmetric to strongly asymmetric; and are interspecially and intraspecially polymorphic in leaf shape and size as well as in cell areolation. Leaves near the branch tips tend to be longer, have more attenuate apices, and have longer and wider cells than leaves lower on the stem. The oldest leaves tend to be shorter, less acuminate, and have broadly rhomboidal cells. Leaf shape varies from elliptical (*L. nitens*) to ovate or oblong-ovate (*L. divaricatum*, *L. isleanum*, and *L. nitens*), ovate-lanceolate (*L. brevisetum* and *L. furcatum*), oblong (*L. brevisetum*, *L. nitens*, *L. devexum*, *L. divaricatum*, *L. furcatum*, *L. isleanum*, and *L. nitens*), oblong-lanceolate (*L. brevisetum*, *L. devexum*, *L. divaricatum*, *L. furcatum*, and *L. nitens*), or lanceolate (*L. furcatum* and *L. nitens*). *Lepidopilidium devexum* has distinctly falcate lateral leaves. The leaf apices are also considerably polymorphic, ranging from acute to short- or long-acuminate. The upper leaf margins are often narrowly recurved, while the lower leaf margins are sometimes broadly infolded at the leaf base. The margins are either elimbate (not bordered) or narrowly bordered, can be entire, serrulate, serrate, or sharply serrate, and have a few swollen or bifurcate teeth (*L. furcatum* and *L. nitens*). The double costae prominently extend to about midleaf and mostly stay parallel, although sometimes they diverge. The costae are smooth, but can be weakly toothed at back, and either do not project at the tips as in *L. devexum* and *L. isleanum* or sometimes project as a short terminal cell as in *L. brevisetum*, *L. divaricatum*, *L. furcatum*, and *L. nitens*.

The sexuality, setae length and ornamentation, capsule shape and orientation, and spore size were emphasized by Brotherus (1907) as taxonomically significant characters in *Lepidopilidium*. The perigonia and perichaetia are produced laterally on the stems and branches, are budlike, and have ovate to lanceolate leaves. Based on sexuality and the distribution of species, *Lepidopilidium* appears to have two distinct lineages. *Lepidopilidium brevisetum* and *L. nitens* are dioicous and occur in the Neotropics, whereas *L. devexum*, *L. furcatum*, and *L. isleanum* are autoicous and occur in the Paleotropics. Only the autoicous species *L. divaricatum* occurs in both tropical regions. Synoicous specimens identified as *L. synoicum* Herzog (= *L. divaricatum*) and *L. theriotii* Naveau (= *L. furcatum*) are morphologically identical to autoicous specimens. The setae vary from short (*L. brevisetum* and *L. furcatum*) to elongate (*L. isleanum* and *L. nitens*) and can be straight, somewhat curved, or flexuous. In addition, the ornamentation varies from smooth throughout (*L. brevisetum*, *L. furcatum*, *L. isleanum*, and *L. nitens*) to smooth below and lightly to densely papillose above (*L. brevisetum*, *L. furcatum*, *L. isleanum*, and *L. nitens*) to densely papillose throughout (*L. devexum* and *L. divaricatum*). Capsule orientation appears to be correlated with setae length. Species with short setae have mostly erect capsules, whereas those with elongate setae have suberect to inclined capsules. This character is somewhat variable depending on the direction that the setae-bearing stems were growing at the time of collection. In some species, such as *L. brevisetum*, *L. devexum*, and *L. furcatum*, both erect and inclined capsules were found on the same plant. Additional characteristics of the capsule as well the opercula, peristome, calyptrae, and spores do not noticeably vary between species.

Key to the Species of *Lepidopilidium*

1a. Lateral leaves broadly ovate, oblong-ovate, or oblong, about 2 to 3 times longer than wide; apices acute to abruptly acuminate and ending in a short or long slender point; apical and median leaf cells hexagonal to broadly rhomboidal, sometimes elongate-rhomboidal.
  2a. Gemmae absent; setae short, 5–7.5 mm long ..... 3. *L. divaricatum* (Dozy & Molk.) Broth.
  2b. Gemmae present; setae elongate, 7–15 mm long.
    3a. Lateral leaves rounded to the insertion; plants autoicous; setae flexuous, densely to lightly papillose throughout, sometimes smooth ..... 5. *L. isleanum* (Besch.) Broth.
    3b. Lateral leaves not rounded to the insertion; plants dioicous; setae straight, smooth or sometimes lightly papillose distally ..... 6. *L. nitens* (Hornsch.) Broth.

1b. Lateral leaves oblong, ovate-lanceolate, oblong-lanceolate or lanceolate, often 3 to 6 times longer than wide; apices gradually short- or long-acuminate; upper leaf cells elongate-rhomboidal or fusiform, sometimes short-rhomboidal.
  4a. Dorsal and ventral leaves slightly dimorphic from lateral leaves; lateral leaves 1.7–3 mm long, not falcate, erect, erect-spreading, or wide-spreading when dry; plants dioicous.
    5a. Setae short, 1–4 mm long ..... 1. *L. brevisetum* (Hampe) Broth.
    5b. Setae longer, 7–15 mm long ..... 6. *L. nitens* (Hornsch.) Broth.
  4b. Dorsal and ventral leaves strongly dimorphic from lateral leaves; lateral leaves 2.6–4 mm long, falcate, spreading to wide-spreading when dry; plants autoicous.
    8a. Setae short, 3–5 mm long, smooth or weakly papillose distally .... 4. *L. furcatum* (Thwaites & Mitt.) Broth.
    8b. Setae longer, 5–7 mm long, papillose throughout ..... 2. *L. devexum* (Mitt.) Broth.

1. Lepidopilidium brevisetum (Hampe) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. Basionym: *Hookeria breviseta* Hampe, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn ser 3, 10: 266. 1878. *Hookeriopsis breviseta* (Hampe) A. Jaeger, Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1877–1878: 510. 1879. TYPE CITATION: [Brazil.] Inter muscos *Glaziovii* pauca specimina carpi. TYPE: [Brazil.] Rio de Janeiro, *A. Glaziou s.n.* (lectotype, designated here, BM!). Figure 1.

Hookeria aureopurpurea Müll. Hal., Hedwigia 39: 278. 1900, nom. illeg. superfl., as "aureo-purpurea," non *Hookeria aureo-purpurea* Geh. & Hampe, Flora 64: 409. 1881. *Lepidopilum aureopurpureum* Müll. Hal., in Ule, Hedwigia 38(Beibl.): 58. 1899, nom. inval. [no description]. Replacement name: *Hookeria lamprophylloides* Paris, Index Bryol. (ed. 2) 2: 336. 1904. *Lepidopilidium lamprophylloides* (Paris) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 687. 1907. TYPE CITATION: Brasilia, Sa. Catharina, Pedras Grandes ad flumen Tubarão superius, in ramulis trunculorum sylvestrium, Aug. 1890, *E. Ule*, Coll. No. *601*; in iisdem locis Junio 1891 c. fr.: idem No. *1183*. TYPE: [Brazil.] Santa Catarina: Tubarão, Aug. 1890, *E. Ule s.n.* (lectotype, designated here, S!; isolectotypes, B!, BR!, FH!, G!, JE!, M!, MO!, PC!, S!, US!).

Lepidopilum fruticola Müll. Hal., Hedwigia 39: 270. 1900, as "fruticolum." *Lepidopilum fruticolum* Müll. Hal., in Ule, Hedwigia 38(Beibl.): 58. 1899, nom. inval. [lacks description]. *Lepidopilidium fruticola* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. *Lepidopilidium fructicosum* (Müll. Hal.) Broth. ex Paris, Coll. Nom. Broth. 17. 1909, orth. var. TYPE CITATION: Brasilia, Sa. Catharina, Serra Geral, in monte Capivare arboretum in declivibus, Januario 1891, *E. Ule*, Coll. No. *1184*; Tubarão, in fruticibus paucis sylvestribus, Julio 1889, idem, Coll. No. *771*, et ad truncos arborum sylvestrium, Aug. 1890, idem, Coll. No. *959*. TYPE: [Brazil.] S. Catarina, Tubarão, "auf Stauden und Gesträuch in eines Waldbache," July 1889, [*Ule*] *771* (lectotype, designated here, H!).

Lepidopilidium brevisetum var. *purpurascens* Broth., in Schiffner (ed.), Ergebn. Bot. Exped. Südbras., Musci 1901, 2: 328. 1924, syn. nov. TYPE CITATION: [Brazil.] São Paulo. In silvis prope Apiahy; ad arbores; ca. 1100 m.s.m. [*Schiffner*] (*1882*). Prope Raiz da Serra; ad arbores in silva; 20–50 m.s.m. [*Schiffner*] (*711*). TYPE: [Brazil.] São Paulo: "In silvis prope Apiahy; ad arbores," ca. 1100 m.s.m., 24 Aug. 1901, *V. Schiffner 1882* (lectotype, designated here, BM!; isolectotype, S!).

Plants glossy, green to golden-brown, sometimes tinted red, in lax mats; stems prostrate, to 4 cm, irregularly and frequently branched, strongly complanate-foliate. Leaves evenly spaced, not or slightly dimorphic, rigid to somewhat flexuous when dry; dorsal and ventral leaves appressed to erect-spreading, symmetric or weakly asymmetric, ovate to oblong, 1.9–2.2 × 0.6–0.8 mm, acute to broadly acuminate; lateral leaves erect to erect-spreading, symmetric or weakly asymmetric, rarely strongly asymmetric, ovate-lanceolate, oblong, or oblong-lanceolate, 1.7–2.5 × 0.5–0.7 mm, gradually acute to broadly or narrowly short-acuminate, occasionally long-acuminate; margins serrate to serrulate above, entire below, plane or narrowly recurved, often broadly folded on one side at base, elimbate; costae extending to midleaf or above, diverging throughout, uneven, smooth, not projecting or weakly projecting at tips; laminal cells smooth, thin-walled; apical and median cells narrowly to broadly fusiform, 35–60 × 10–18 μm, becoming oblong and elongate below; basal cells enlarged, oblong-rectangular. Gemmae present. Plants dioicous. Setae straight or curved, 1–4 mm, yellow to red, smooth or lightly papillose above; capsules erect to suberect, obloid, 1 mm long; opercula short conic-rostrate, 0.8 mm long. Spores 24–30 μm, yellow, finely papillose. Calyptrae 1.7–2 mm long.

Iconography. Brotherus (1907: 244, fig. 605, as *Lepidopilidium lamprophylloides* (Paris) Broth.); Sehnem (1979: 77, tab. IX, fig. b, as *L. brevisetum* (Hampe) Broth.); Vaz and Costa (2006: 979, figs. 1–6, as *L. aureopurpureum* (Geh. & Hampe) Broth.); Vaz-Imbassahy and Costa (2008: 562, figs. 90–95, as *L. aureopurpureum* (Geh. & Hampe) Broth.).

Habitat and distribution. *Lepidopilidium brevisetum* is known from the Brazilian states of Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo, where it has been collected on leaves and the branches of trees and treelets in humid forests, often near water at 100–1200 m elevation (Fig. 2A).

Nomenclatural notes. Among the numerous mosses described by Hampe based on the Rio de Janeiro

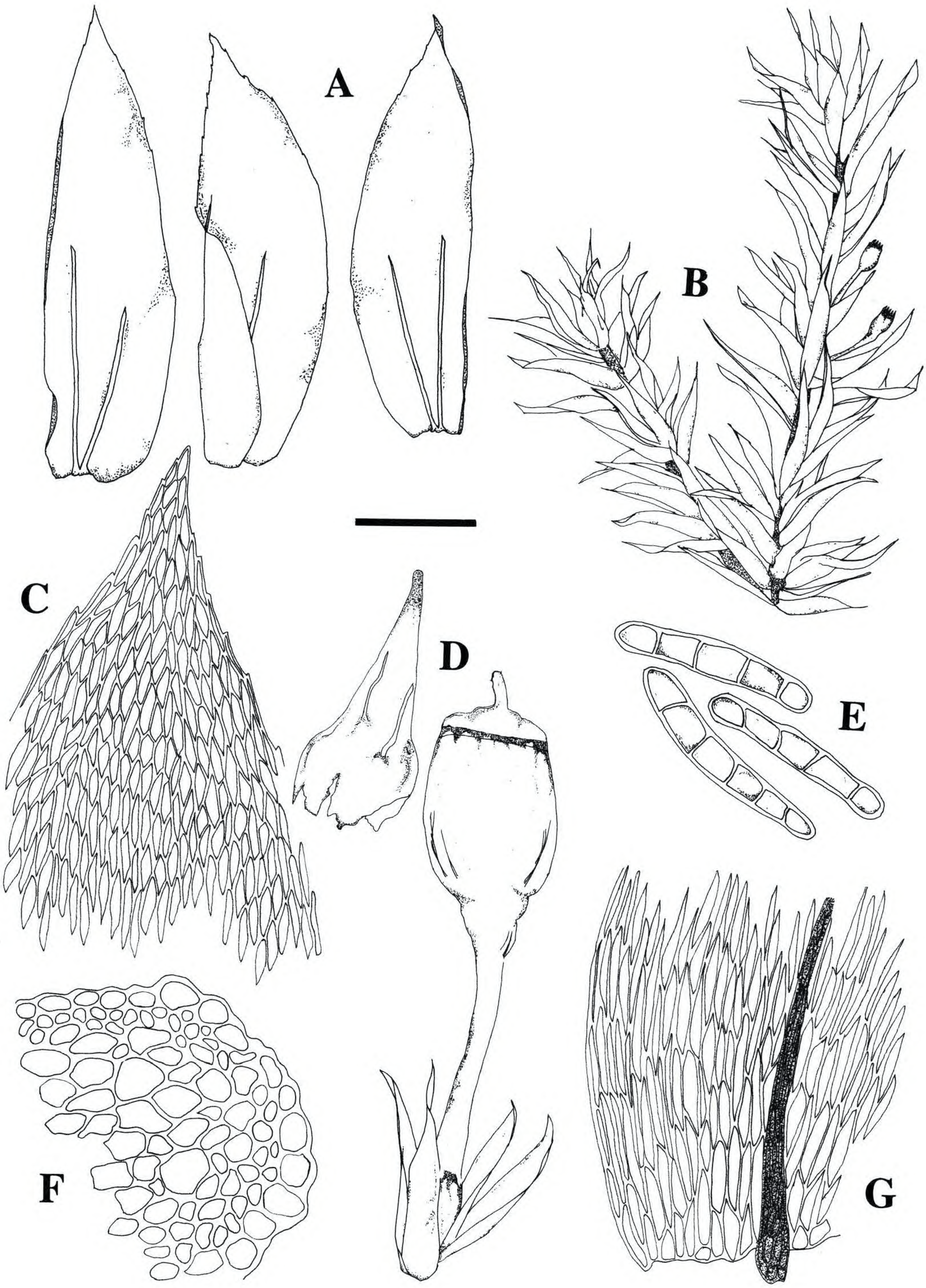


Figure 1. *Lepidopilidium brevisetum* (Hampe) Broth. —A. Lateral leaves. —B. Habit with sporophytes. —C. Lateral leaf apex. —D. Calyptra and sporophyte. —E. Gemmae. —F. Transverse section of stem. —G. Basal laminal cells of lateral leaf. Scale bars: A = 0.6 mm; B = 1.96 mm; C, E, G = 0.13 mm; D = 0.8 mm; F = 0.06 mm. A, C, D, F, G drawn from *Vital & Buck 20584* (MO); B, E drawn from *Bandeira 454* (MO, NY).

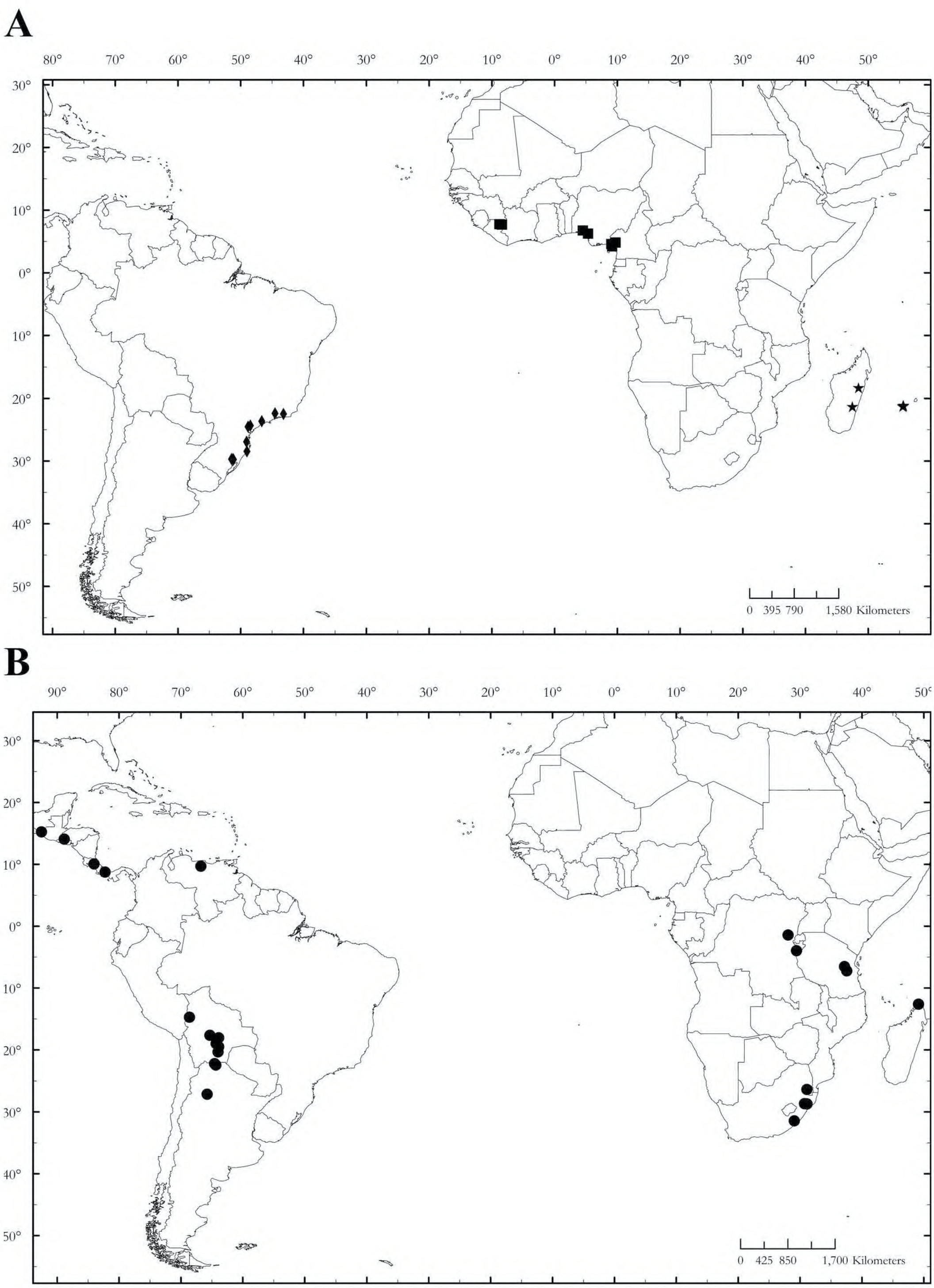


Figure 2. Distributions of *Lepidopilidium* (Müll. Hal.) Broth. species. —A. *Lepidopilidium brevisetum* (Hampe) Broth. (♦), *Lepidopilidium devexum* (Mitt.) Broth. (■), *Lepidopilidium isleanum* (Besch.) Broth. (★). —B. *Lepidopilidium divaricatum* (Dozy & Molk.) Broth. (●).

collections of Glaziou are two species now placed in *Lepidopilidium*. Hampe (1878) described *Hookeria breviseta* [≡ *Lepidopilidium brevisetum*] from a small specimen separated from one of Glaziou's collections. The single specimen lacks a collection number and is in Hampe's herbarium, now deposited in BM. The specimen label as well as the herbarium sheet have Hampe's notes; the specimen appears to be the only one used in the description of the new species. This specimen is selected as the lectotype. The second species, described by Hampe (1879) and now placed in *Lepidopilidium*, is *Lepidopilum laevisetum* [= *Lepidopilidium nitens*]. On some labels the epithet has been misread and reprinted as "brevisetum," although the correlating specimens do not match the type description of *Lepidopilidium brevisetum*.

Hookeria aureopurpurea was described by Müller (1900) on the basis of two syntypic specimens collected by Ule (*601* and *1183*). Among the Ule specimens examined in this study, none had either collection number. Much of the information in Müller's type citation for *Ule 601* matches that on the label of exsiccatal specimen No. *94* (as *Lepidopilum aureopurpureum*) in Ule's (1899) *Bryotheca Brasiliensis*. Specimens in B, BR, FH, G, M, MO, PC, S, and US have "Sa. Catharina, Tubarão" as well as the abbreviated month and year "Aug. 1890." Despite the absence of Ule's collection number *601*, the exsiccatal duplicates are original material. A particularly large specimen with numerous sporophytes in S is designated as the lectotype.

Müller (1900) described *Lepidopilum fruticola* (as "fruticolum") based on three syntypic specimens collected by Ule. The first of these, *Ule 1184*, was cited by Churchill (1988) as belonging to another species, *Lepidopilum subsubulatum* Geh. & Hampe. Another specimen, *Ule 959*, is better identified as *Lepidopilidium nitens*. Only specimen *Ule 771* consistently matches the type description of *Lepidopilum fruticola* and is therefore selected as the lectotype.

Syntype specimens of *Lepidopilidium brevisetum* var. *purpurascens* were both collected from São Paulo, Brazil, in 1901 by Schiffner. These were known to be deposited in BM and S, but were not located in the describing author's herbarium in H. Both specimens equally match the brief type diagnosis. *Schiffner 1882* is selected as the lectotype because it is larger than *Schiffner 711* and has sporophytes.

Discussion. *Lepidopilidium brevisetum* has ovate-lanceolate, oblong or oblong-lanceolate lateral leaves, mostly broad to narrowly short-acuminate apices, and serrate to serrulate upper leaf margins. The costae extend to midleaf or above, are smooth, or occasionally project at the tips. The apical and median laminal cells range from broadly to narrowly fusiform. The setae are short, and the obloid capsules are mostly erect. The only other *Lepidopilidium* species with similarly short setae and mostly erect capsules is *L. furcatum*. That species, however, occurs in Africa, Madagascar, southern India, and Sri Lanka. *Lepidopilidium brevisetum* further differs from *L. furcatum* in dioicous versus autoicous or synoicous plants, less differentiated dorsal, ventral, and lateral leaves, and shorter (1.7–2.5 mm vs. 2.6–4 mm), more symmetrical leaves, with less sharply toothed upper leaf margins. Superficially, *L. brevisetum* is more likely to be confused with *Lepidopilum* species that have strongly complanate-foliate stems, short setae, and erect capsules, such as *L. brevipes* Mitt., *L. cuspidans* Mitt., and *L. subsubulatum*. Although the discernibly different setae ornamentation and peristome will separate the two genera, sterile and mixed specimens can be particularly difficult to differentiate. Ule's (1899) *Bryotheca Brasiliensis* exsiccatal specimen No. *74* is one such mixture. Specimens in BM, H, NY, and S belong mostly to type material of *Lepidopilum nanothecium* Müll. Hal. [= *Lepidopilum brevipes*], whereas specimens in L and S belong mostly to *Lepidopilum fruticola* [= *Lepidopilidium brevisetum*]. Sterile stems in this mixture can be differentiated by the spacing of the lateral leaves when dry. Dry lateral leaves of *Lepidopilidium brevisetum* are more closely spaced and erect-spreading in comparison to the dry lateral leaves of *Lepidopilum brevipes*, which are distantly spaced and wide-spreading.

Vaz and Costa (2006) and Vaz-Imbassahy and Costa (2008) considered the invalid homonym *Lepidopilum aureopurpureum* [≡ *Lepidopilidium lamprophylloides*] to be a synonym of *Lepidopilidium aureopurpureum* (Geh. & Hampe) Broth. However, the type of *Lepidopilidium lamprophylloides* has short setae and erect capsules, whereas the type of *Lepidopilidium aureopurpureum* (as *Hookeria aureopurpurea*) has elongate setae and suberect to inclined capsules and is a synonym of *L. nitens*. Their taxonomic concept of *Lepidopilidium aureopurpureum* otherwise agrees with the concept of *L. brevisetum* presented here. Conversely, their concept of *L. brevisetum* matches the concept of *L. nitens* presented here.

Lepidopilidium brevisetum var. *purpurascens* was described by Brotherus (1924) for two specimens having dark red–colored leaves. Apart from color, pigmented and non-pigmented leaves are morphologically inseparable, and such mixtures can often be found on the same plant.

Additional specimens examined. BRAZIL. **Rio de Janeiro:** Itatiaia, *Bandeira 454* (MO, NY); Tijuca, *Ule 160* (PC). **Rio Grande do Sul:** São Leopoldo, Rio dos Sinos, *Sehnem 198* (FH, NY). **Santa Catarina:** Pedras Grandes, *Ule 691* (PC). **São Paulo:** Apiahy, Sep. 1880, *Puiggari s.n.* (JE), *53b* (G, MO), *631* (JE, L, S); Blumenau, *Ule* [Bryoth. Brasil.] *74*, pro parte (L, S); Iporanga, Serra Paranapiacaba, Faz. Intervales, Rio do Carmo, *Vital & Buck 20584* (MO, NY, SP); Prope Raiz da Serra, *Schiffner 711* (syntype, *Lepidopilidium brevisetum* var. *purpurascens*, BM!).

2. Lepidopilidium devexum (Mitt.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. Basionym: *Lepidopilum devexum* Mitt., J. Proc. Linn. Soc., Bot. 7: 159. 1863. TYPE CITATION: Cameroons Mtn., alt. 4000 ft., *Mann*. TYPE: Cameroon. Cameroon Mtn., 4000 ft., Feb. 1862, *Mann s.n.* (lectotype, designated here, NY!; isotypes, BM!, MO!). Figure 3.

Lepidopilum subdevexum Broth., Bot. Jahrb. Syst. 24: 260. 1897, syn. nov. *Lepidopilidium subdevexum* (Broth.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Kamerun. an Baumästen bei Ekundu Etitti (*Dusén*). TYPE: Cameroon. "ad Ekundu Etitti emporium," Aug. 1890, *P. Dusén s.n.* (lectotype, designated here, H!; isotypes, BR!, PC!).

Lepidopilum leiopus Müll. Hal., in Paris, Index Bryol. 723. 1898, nom. inval. [lacks description], syn. nov. TYPE: Cameroon. *Dusén* [Musci Africani in Camerunia] *358* (S!).

Plants glossy, golden-yellow, brown to dark red, in lax mats; stems prostrate, to 6 cm, sparsely branched, strongly complanate-foliate. Leaves evenly spaced, somewhat folded, dimorphic; dorsal and ventral leaves appressed, symmetric to weakly asymmetric, ovate-lanceolate, 2–2.7 × 0.6–0.8 mm, short-acuminate; lateral leaves wide-spreading when dry and wet; asymmetric, oblong to oblong-lanceolate, falcate, 2.7–3.3 × 0.5–0.8 mm, narrowly short- to long-acuminate; margins plane or narrowly recurved, often broadly folded on one side at base, sharply serrate above, becoming serrulate to entire below, obscurely bordered by 1 to 2 rows of narrow, elongate cells, confluent at apices; costae extending to midleaf, diverging throughout; uneven, smooth at back, not projecting to weakly projecting at tips; laminal cells smooth, thin-walled; apical and median cells narrowly rhomboidal to fusiform 50–100 × 16–24 μm, becoming elongate-fusiform below. Gemmae absent. Plants autoicous or synoicous. Setae straight or curved, 5–7 mm, yellow to red, papillose throughout; capsules suberect, inclined, or occasionally erect, obloid, 1.3–1.6 mm long, often constricted below the mouth when dry; opercula conic-rostrate, 0.8 mm long. Spores 25–30 μm, yellow, finely papillose. Calyptrae 1.5–1.8 mm long.

Habitat and distribution. *Lepidopilidium devexum* is known from the mountainous regions of western Africa in Guinea, Nigeria, and Cameroon. The species has been collected on branches, twigs, and leaves of shrubs and trees at 1000–1200 m elevation (Fig. 2A).

Nomenclatural notes. *Lepidopilum devexum* was described by Mitten (1863) from a collection made by Mann on the summit of Mount Cameroon, Cameroon. Duplicates of this specimen are deposited in BM, MO, and NY. The specimen in Mitten's herbarium in NY includes accompanying illustrations and is designated as the lectotype.

Original material of *Lepidopilum subdevexum*, described by Brotherus (1897), is represented in BR, H, and PC. The specimen in Brotherus's herbarium in H is the largest of the three duplicates and is designated as the lectotype.

The name *Lepidopilum leiopus* is based on Dusén's *Musci Africani in Camerunia* No. *358*, which lacked a validating description and was excluded from *Lepidopilum* by Churchill (1988). An annotated specimen in S includes a note by Brotherus comparing *L. leiopus* to *Lepidopilidium subdevexum*, a name now synonymous with *Lepidopilidium devexum*. His disposition is followed here.

Discussion. *Lepidopilidium devexum* has strongly complanate-foliate stems, asymmetric, oblong to oblong-lanceolate lateral leaves, with narrowly short- to long-acuminate apices. The species is similar to *L. divaricatum* in having plants autoicous or synoicous with papillose setae 5–7 mm long and obloid, mostly suberect to inclined capsules. *Lepidopilidium devexum* differs in having distinctly wide-spreading lateral leaves that are longer (2.7–3.3 mm vs. 2.2–2.7 mm) and narrower (0.5–0.8 mm vs. 1–1.3 mm). Although the lateral leaves of *L. devexum* overlap in size with *L. furcatum*, that species can be differentiated by its longer leaf apices and shorter, smooth to distally papillose setae. Brotherus (1897) used the name *L. subdevexum* to describe one of Dusén's specimens from Cameroon that was similar to *L. devexum* but had erect, instead of inclined, capsules. In a later treatment of *Lepidopilidium*, Brotherus (1907) emphasized capsule orientation as well as the curvature of the setae as taxonomically important characters. In comparing the types of *L. devexum* and *L. subdevexum*, the differences in capsule orientation and curvature of the setae are readily noticeable. However, considerable variation has been observed in the examination of additional specimens. Both species have setae that curve under the base of the capsule urn, resulting in a mixture of erect, suberect,

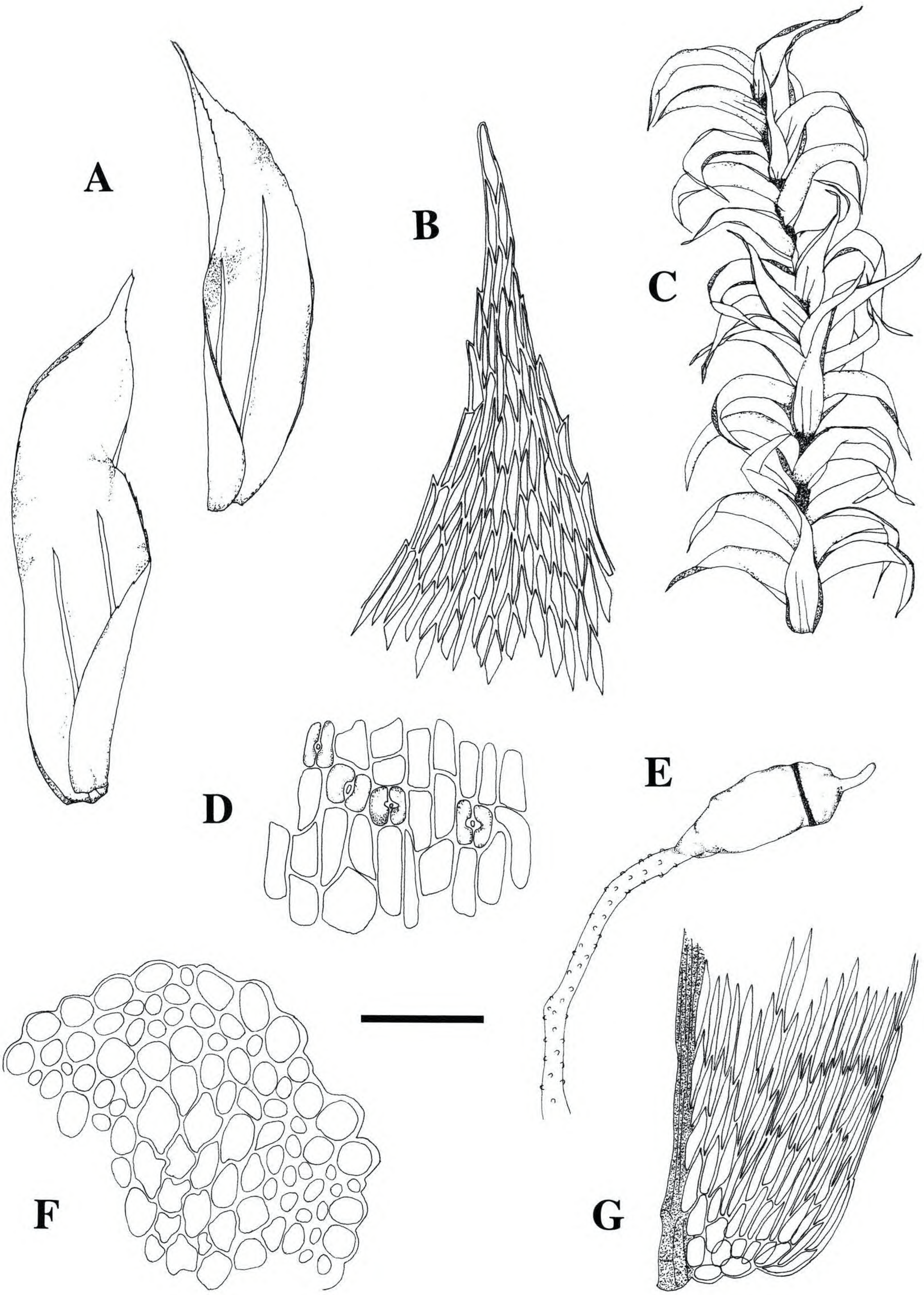


Figure 3. *Lepidopilidium devexum* (Mitt.) Broth. —A. Lateral leaves. —B. Lateral leaf apex. —C. Habit. —D. Stomata. —E. Sporophyte. —F. Transverse section of stem. —G. Basal laminal cells of lateral leaf. Scale bars: A = 0.6 mm; B, G = 0.13 mm; C = 1.96 mm; D = 0.6 mm; E = 0.8 mm; F = 0.06 mm. A, B, F, G drawn from *Brenan et al. 3910* (MO); C–E drawn from lectotype, *Mann s.n.* (NY).

and inclined capsules. Capsule orientation appears to be related to the direction the setae-bearing stems were growing at the time of collection, and particularly large specimens, such as the isotype of *L. devexum* in BM, exhibit a mixture of capsule orientations.

Additional specimens examined. CAMEROON. **Southwest:** N of Mount Koupe, above Nyassosso, ca. 15 km N of Tombel, *Magill & Crosby 9114a* (MO). GUINEA. **Nzérékoré:** Mount Nimba Strict Nature Reserve, *Allen 30751A* (MO), *Baldwin 13180* (FH), *13183* (FH). NIGERIA. **Bendel:** Okomu Forest Reserve, *Richards 3288* (MO), *3611* (MO), *3910* (MO). **Ogun:** Shasha Forest Reserve, near Akilla, *Richards 3140* (MO), *3502* (MO).

3. Lepidopilidium divaricatum (Dozy & Molk.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. Basionym: *Hookeria divaricata* Dozy & Molk., Prodr. Fl. Bryol. Surinam. 49. 13. 1854. *Lepidopilum divaricatum* (Dozy & Molk.) Mitt., J. Linn. Soc., Bot. 12: 379. 1869. TYPE CITATION: In Venezuela, juxta Rio Catuche, ubi collegit *P. W. Korthals*. TYPE: Venezuela. *Korthals s.n.* (lectotype, designated here, L!; isotypes, BM!, NY!, US!). Figure 4.

Lepidopilum corbieri Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 85. 1905, syn. nov. *Lepidopilidium corbieri* (Renauld & Cardot) Cardot, in Grandidier, Hist. Phys. Madagascar, Mousses 413. 1915. *Hookeriopsis corbieri* (Renauld & Cardot) Broth. ex Cardot, in Grandidier, Hist. Phys. Madagascar, Mousses 413. 1915, nom. inval., pro syn. TYPE CITATION: Madagascar. Montagne d'Ambre près Diego Suarez, *Leloutre*, 1899 (Hb. Corbière). TYPE: Madagascar. Montagne d'Ambre près Diego Suarez, 1899, *Leloutre s.n.* (lectotype, designated here, PC!).

Lepidopilum subdivaricatum Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 32(1): 195. 1894. *Lepidopilidium subdivaricatum* (Renauld & Cardot) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: [Costa Rica.] s.l. (*Pitt.* No. *5658*). TYPE: Costa Rica. s. loc., *Pitt. 5658* (lectotype, designated here, PC!; isotypes, BR!, FH!, NY!).

Lepidopilidium synoicum Herzog, Biblioth. Bot. 87: 134. 1916. TYPE CITATION: [Bolivia.] An feuchten Steinen in der Quebrada de Pocona, ca. 2800 m, [*Herzog*] No. *5140*. TYPE: [Bolivia.] "Auf feuchten Steinen in der Quebrada de Pocona," ca. 2800 m, Apr. 1911, [*Herzog*] *5140* (lectotype, designated here, M!; isotypes, L!, PC!).

Plants yellowish, dull or dark green, occasionally tinted red, in lax mats; stems prostrate, to 7 cm, sparsely to irregularly branched, strongly complanate-foliate. Leaves evenly spaced, strongly dimorphic, flattened or flexuous-contorted; dorsal and ventral leaves erect, symmetric, ovate or oblong-ovate, short-acute to slenderly acuminate; lateral leaves loosely spreading, asymmetric, broadly ovate, oblong-ovate, obovate, oblong, or oblong-lanceolate, 2.2–2.7 × 1–1.3 mm, acute to abruptly and slenderly short-acuminate or occasionally long-acuminate; margins serrulate to serrate above, entire below, plane or recurved, often broadly infolded on one side at base, elimbate or bordered by 1 or 2 rows of elongate narrow cells; costae extending to midleaf or below, diverging throughout, uneven; laminal cells smooth, thin-walled; apical and median cells hexagonal to broadly rhomboidal 60–100 × 10–18 μm, becoming elongate-rhomboidal to rectangular below, basal cells enlarged, rectangular. Gemmae absent. Plants autoicous or synoicous. Setae straight or curved, 5–7.5 mm, red-brown, papillose throughout; capsules erect, suberect, or inclined, obloid-cylindrical, 0.5–1 mm long; opercula short conic-rostrate, 0.8 mm long; Spores 12–20 μm, yellow, finely papillose. Calyptrae 1.7–2 mm long.

Iconography. Dozy and Molkenboer (1854: 52, tab. 13, figs. 1–21, as *Hookeria divaricata* Dozy & Molk.); Renauld (1909: tab. 21, fig. 1, as *Lepidopilum corbieri* Renauld & Cardot); Renauld and Cardot (1915: tab. 97A, fig. 1a–e, as *Lepidopilum corbieri* Renauld & Cardot); Welch (1971: 115, figs. 173–181, as *Lepidopilidium divaricatum* (Dozy & Molk.) Broth.; 1974: 372, figs. 279–289, as *Lepidopilidium subdivaricatum* (Renauld & Cardot) Broth.); De Sloover (1975: 121, figs. 75–82, as *Lepidopilidium corbieri* (Renauld & Cardot) Cardot); Gradstein et al. (2001: 451, fig. 168A–C, as *Lepidopilidium divaricatum* (Dozy & Molk.) Broth.); Allen (2010: 545, fig. 185, as *Lepidopilidium divaricatum* (Dozy & Molk.) Broth.).

Habitat and distribution. *Lepidopilidium divaricatum* is present in southern Mexico; Central America; northern, western, and southern South America; eastern and southern Africa; and Madagascar. The species has been collected on trunks and branches of trees as well as on logs and rocks at 600–2700 m elevation (Fig. 2B).

Nomenclatural notes. Dozy and Molkenboer (1854) described *Hookeria divaricata* from an unnumbered specimen collected by Pieter Korthals in Venezuela. Duplicates of the original material are located in BM, L, NY, and US. The specimen in Dozy and Molkenboer's herbarium, deposited in L, is designated as the lectotype.

Lepidopilum corbieri was described from an unnumbered specimen collected in Madagascar by Leloutre in 1899. The type citation notes the specimen to be deposited in Corbiere's herbarium, now in CHE. Original material in Cardot's herbarium, now in PC, agrees with the specimen information cited in the 1905 protologue by Renauld and Cardot

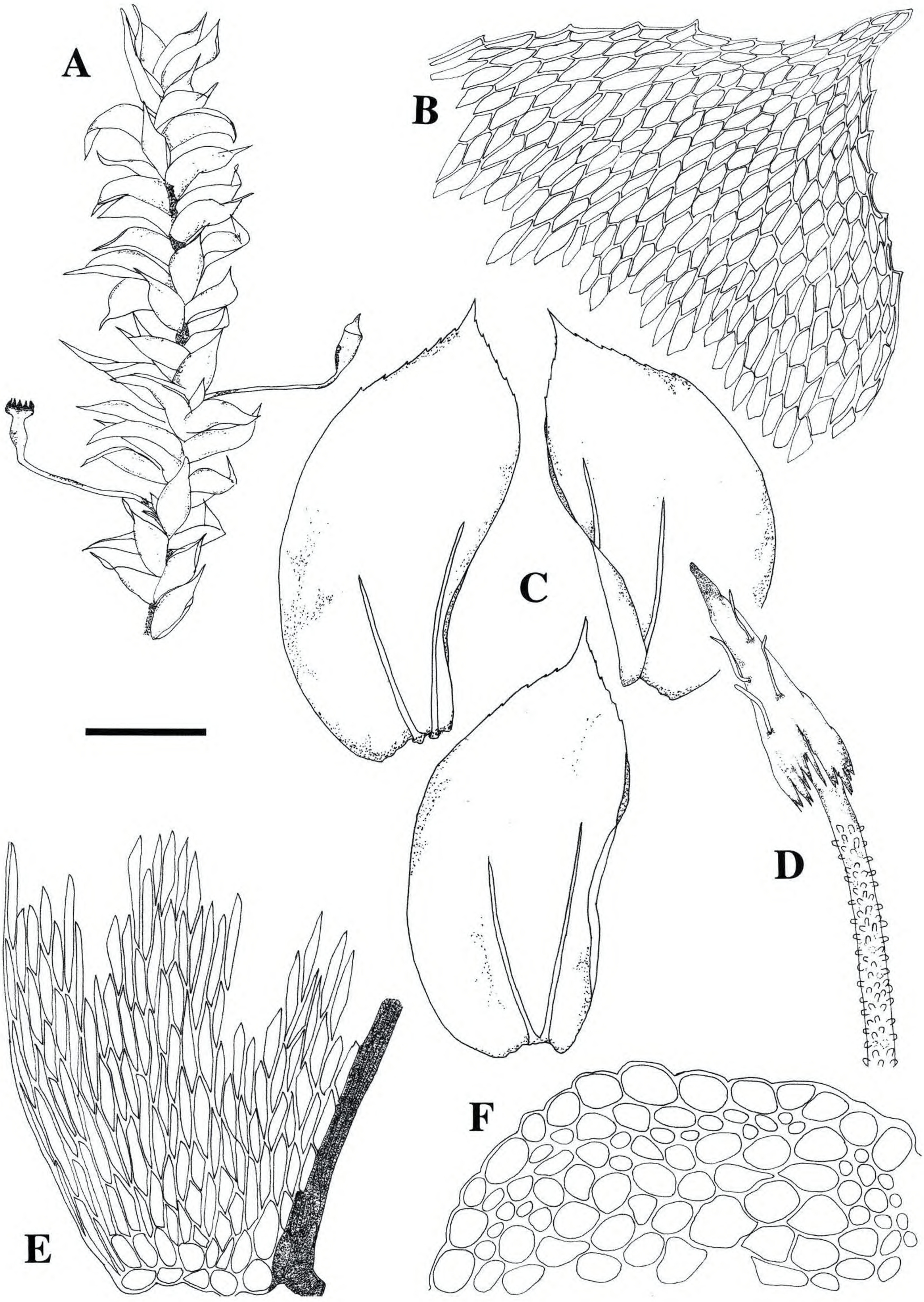


Figure 4. *Lepidopilidium divaricatum* (Dozy & Molk.) Broth. —A. Habit with sporophytes. —B. Lateral leaf apex. —C. Lateral leaves. —D. Sporophyte. —E. Basal laminal cells of lateral leaf. —F. Transverse section of stem. Scale bars: A = 1.96 mm; B, E = 0.13 mm; C = 0.6 mm; D = 0.8 mm; F = 0.06 mm. A, D drawn from *Crosby 9932* (MO); B, C, E, F drawn from *Crosby 7529* (MO).

and also has "Hb. Corbière" noted on the label. The PC specimen is designated as the lectotype.

Lepidopilum subdivaricatum was described in 1894 by Renauld and Cardot from the specimen *Pitt 5658* that was collected in Costa Rica without locality. Syntypic material is located in BR, FH, NY, and PC. The specimen in Cardot's herbarium in PC is designated as the lectotype.

Lepidopilidium synoicum was described by Herzog (1916) based on the specimen *Herzog 5140* from Bolivia. Original material of *L. synoicum* is located in L, M, and PC. Since part of Herzog's personal herbarium is deposited in M, the specimen in the author's herbarium is designated as the lectotype.

Discussion. *Lepidopilidium divaricatum* has mostly asymmetric oblong-ovate to oblong lateral leaves, although the shape can vary between broadly ovate, obovate, or oblong-lanceolate. The apices are acute to abruptly acuminate and end in short to long, slender points. The leaf margins are often obscurely bordered by one or two rows of narrow, elongate cells and are usually serrulate to serrate above. The costae extend to midleaf or below, and the apical and median leaf cells are mostly hexagonal to broadly rhomboidal. *Lepidopilidium divaricatum* is the only species in the genus currently found in both the Americas and Africa. The strongly complanate-foliate habit, autoicous or synoicous plants, and densely papillose setae separate this from all other American *Lepidopilidium* species. Among the African species, *L. divaricatum* differs from *L. devexum* in having less spreading, more contorted-flexuous leaves as well as more abruptly and slenderly acuminate leaf apices. *Lepidopilidium isleanum* has similarly oblong, short-acuminate lateral leaves with differentiated marginal borders, although it has longer (10–17 mm vs. 5–7.5 mm), flexuous setae, with a partially smooth ornamentation. *Lepidopilidium furcatum* also overlaps somewhat in lateral leaf shape and size with *L. divaricatum*. Although most specimens of *L. divaricatum* tend to have shorter and broader lateral leaf apices, specimens collected from twigs are more elongate and have apices that approach those of *L. furcatum*. Setae length and ornamentation best distinguish these two species. The setae of *L. divaricatum* are mostly longer than those of *L. furcatum* (5–7.5 mm vs. 3–5 mm) and are densely furnished with papillae. In comparison, the setae of *L. furcatum* are mostly smooth throughout, except for some scattered, low papillae present beneath the capsule.

Additional specimens examined. COSTA RICA. **Heredia:** Volcán Barba, ca. 1 km WNW of Río Ciruelas, *Crosby 9932* (MO); Las Vueltas area, *Crosby 13119* (MO), *13120* (MO). HONDURAS. **Comayagua:** San Juanillo, Cordillera de Montecillos Biol. Reserve, 12 km S of Siguatepeque, *Allen 12308* (MO), *12331* (MO); along Agua Amarilla, ca. 11 km E of Lake Yojoa, *Allen 13966* (MO). **Ocotepeque:** Montana del Candado, 13 km E of Nueva Ocotepeque & Cerro El Cocal, 12 km NE of Nueva Ocotepeque, *Allen 14488* (MO). MEXICO. **Chiapas:** Yerba Buena, Pueblo Nuevo, *Smith 2845a* (MO). PANAMA. **Chiriquí:** Valle de la Siërpe, *Salazar 5749a* (MO).

ARGENTINA. **Tucumán:** Dpto. Monteros, Río Pueblo Viejo por Quebrada del Portugues, *Churchill & Schiavone 20082* (MO), *20100* (MO). BOLIVIA. **Chuquisaca:** Belisario Boeto, Nuevo Mundo, *Lozano 957* (MO); Hernando Siles, Cañón Lacayotal, *Lozano et al. 1799* (MO); Luis Calvo, Serranía del Iñao, *Lozano & Mogro 159* (MO). **La Paz:** Santa Barbara, Apolo region, *Williams 2879* (NY). **Santa Cruz:** Florida, Mpio. Mairana, ca. 4 km NE de Las Yungas, finca de Don Lelide Cardona, *Churchill et al. 23799* (MO), *23808* (MO), *23814* (MO). **Tarija:** Arce, Reserva Natural Alarachi, Zona Alarachi, Baden Chico, *Churchill et al. 23346* (MO); Arce, Mpio. Padcaya, Cantón Emborozú, Reserva Natural Alarachi, *Churchill et al. 23459* (MO), *23463* (MO), *23474* (MO); Arce, Reserva Nac. de Flora de Fauna Tariquía Piedemonte serranía San Telmo, *Serrano et al. 5852* (MO). VENEZUELA. **Distrito Federal:** Caracas, *Ernst 12213* (MO).

DEMOCRATIC REPUBLIC OF THE CONGO. **North Kivu:** *Boutakoff s.n.* (BR). REPUBLIC OF BURUNDI. **Bururi:** Bord do lac Tanganyika, *De Sloover 19230* (BR). TANZANIA. **Dodoma:** Kiboriani Mtns., NE face of highest peak about Mpwapwa, *Pócs & Mezösi 6569/O* (MO). **Morogoro:** Uluguru Mtns., NW slopes of Palata, 9 km SSE of Morogoro, *Crosby & Pócs 8690* (MO); Uluguru Mtns., NW slopes of main ridge of Lupanga, *Pócs & Harris 6129/B* (L, MO); N Uluguru Mtns., Lupanga-Kinazi ridge, *Pócs & Mwanjabe 6836/AV* (MO). SOUTH AFRICA. **Eastern Cape:** Transkei, Mlanlane Forest Station, *van Rooy 2223* (MO). **Kwazulu-Natal:** Nkandla Forest Reserve, *Magill 5176* (MO), *5220* (MO), *5225* (MO, NY), *van Rooy 118* (MO, NY); Qudeni Forest, *Magill 5109* (MO, NY), *5145* (MO); Dhlinza Forest Reserve, *Crosby 7786* (L, MO). SWAZILAND. **Hhohho:** 5.5 km SW of Mbabane, *Kemp 1499* (MO).

4. **Lepidopilidium furcatum** (Thwaites & Mitt.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. Basionym: *Lepidopilum furcatum* Thwaites & Mitt., in Mitten, J. Linn. Soc., Bot. 13: 310. 1873. TYPE CITATION: Ins. Ceylon. *Dr. Thwaites*. TYPE: [Sri Lanka.] "Cent. Prov. Ceylon." *Thwaites s.n.* (lectotype, designated here, NY!; isotypes, BM!, FH!, G!, H!, MO!, NY!). Figure 5.

Lepidopilum hanningtonii Mitt., J. Linn. Soc., Bot. 22: 309. 1886, syn. nov. *Lepidopilidium hanningtonii* (Mitt.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Usagara Mtns., *Bishop Hannington*. TYPE: [Tanzania.] Usagara Mtns., Oct. 1883, *Hannington s.n.* (lectotype, designated here, NY!; isotypes, BM!, NY!).

Lepidopilidium attenuatum Thér., Recueil Publ. Soc. Havraise Études Diverses 1929: 117. tab. s.n. 1930, syn. nov. TYPE CITATION: Andasibe, sur petites branches d'arbres. TYPE: Madagascar. "Forêt d'Andasibe sur l'Onive," Feb. 1925, *P. de la Bâthie s.n.* (lectotype, designated here, PC!; isotype, BR!).

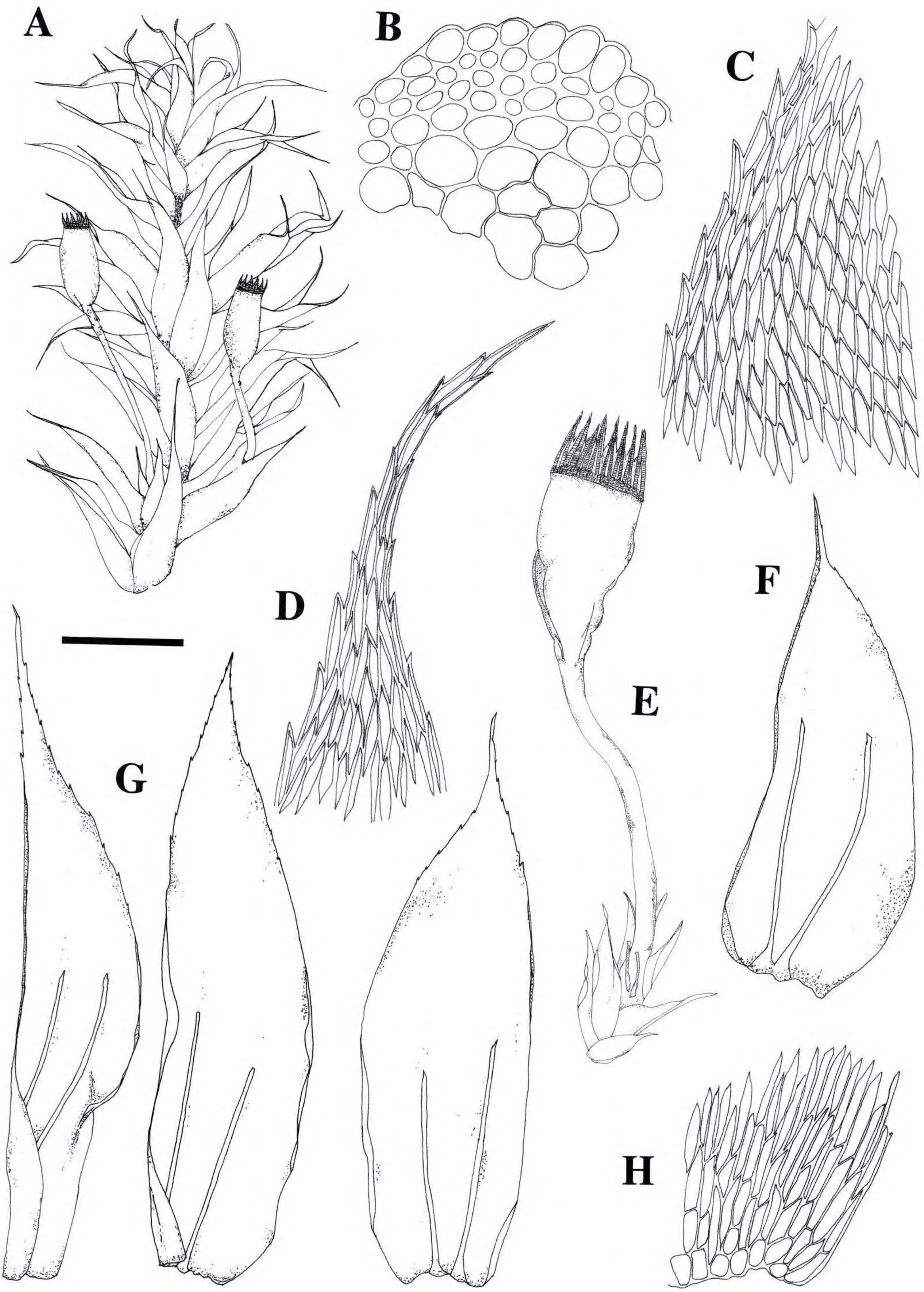


Figure 5. *Lepidopilidium furcatum* (Thwaites & Mitt.) Broth. —A. Habit with sporophytes. —B. Transverse section of stem. —C. Median laminal cells of lateral leaf. —D. Lateral leaf apex. —E. Sporophyte. —F. Dorsal leaf. —G. Lateral leaves. —H. Basal laminal cells of lateral leaf. Scale bars: A = 1.96 mm; B = 0.06 mm; C, D, H = 0.13 mm; E = 0.8 mm; F, G = 0.6 mm. A, F, G drawn from *Crosby 14437* (MO); B–D, H drawn from *De Sloover 12913* (MO); E drawn from lectotype, *Bequaert 4743 bis* (BR).

Lepidopilidium theriotii Naveau, in Dixon & Thériot, Mélanges Bryol. Lichénol. 74. 1942, syn. nov. TYPE CITATION: Ruvenzori, Lanuri, 2.500 m, sur bamboo; leg. Dr. *Bequaert*, mai 1914 [*Bequaert*]. TYPE: [Democratic Republic of the Congo.] Ruvenzori (Lanuri) ± 2500 m, sur bambou, 18 May 1914, *Bequaert 4743 bis* (lectotype, designated here, BR!; isotypes, BR!, JE!, PC!).

Lepidopilidium subdevexum (Broth.) Broth. var. *intermedium* P. de la Varde, Rev. Bryol. Lichénol. 11: 183. 1939, syn. nov. TYPE CITATION: [l'Oubangui, Région de Berbérati] Sur brindilles près d'un ruisseau, forêt de la mission [*R. P. C. Tisserant*]. TYPE: [Central African Republic.] Oubangui, sur rameaux et feuilles au dessus de l'eau ruisseau dans la forêt de Berbérati, 6 June 1937, *R. P. Tisserant s.n.* (lectotype, designated here, PC!; isotypes, BR!, PC!).

Plants glossy, yellowish green to golden, sometimes tinted red, in loose to dense mats or tufts; stems prostrate or erect, to 7 cm, frequently branched, moderately complanate-foliate. Leaves crowded, strongly dimorphic; dorsal and ventral leaves erect to erect-spreading, symmetric, ovate-oblong to oblong-lanceolate, abruptly acuminate; lateral leaves spreading to wide-spreading, asymmetric, ovate-lanceolate, oblong, oblong-lanceolate, or lanceolate, 2.6–4 × 0.6–1 mm, narrowly short- to long-acuminate, sometimes tapering into a long point; margins serrate to sharply serrate above, becoming serrulate to entire below, plane or narrowly recurved, elimbate; costae extending to midleaf or above, sometimes projecting at the tips; laminal cells smooth, thin-walled; apical and median cells rhomboidal to narrowly or broadly fusiform, 60–100 × 10–18 μm, sometimes linear-elongate becoming oblong-rectangular to oblong-fusiform below, basal cells enlarged, rectangular. Gemmae present. Autoicous or synoicous. Setae straight or curved, 3–5 mm, red, smooth throughout or smooth below to lightly or densely papillose above. Capsules erect, sub-erect, or inclined, obloid, 1–1.3 mm long; opercula conic, 0.6 mm long. Spores 17–25 μm, yellow, finely papillose. Calyptrae 1.7–2 mm long.

Iconography. Abeywickrama (1960: 96, figs. 112a–c, as *Lepidopilidium furcatum* (Thwaites & Mitt.) Broth.); Thériot (1930: 118, figs. 1–10, as *L. attenuatum* Thér.); De Sloover (1975: 119, figs. 65–74, as *L. theriotii* Naveau); Magill and van Rooy (1998: 610, fig. 169, 1–13, as *L. hanningtonii* Mitt.).

Habitat and distribution. *Lepidopilidium furcatum* is known across central and south tropical Africa; southern Africa; Madagascar; southern India, and Sri Lanka. It has been collected on the trunks, branches, and twigs of trees and shrubs, also on leaves and vines, and occasionally on moist boulders at 300–2300 m elevation (Fig. 6A).

Nomenclatural notes. Thwaites and Mitten described *Lepidopilum furcatum* in 1873 from an unnumbered collection made by Thwaites in Sri Lanka. Original material is deposited in BM, FH, G, H, MO, and NY, among duplicates. A duplicate in Mitten's herbarium in NY includes accompanying illustrations and is designated as the lectotype.

Lepidopilum hanningtonii was described by Mitten based on an unnumbered collection made by Hannington in Tanzania. A particularly large specimen in NY, with accompanying illustrations, is designated as the lectotype.

Thériot (1930) described *Lepidopilidium attenuatum* based on a collection made by Perrier de la Bâthie in Madagascar. Syntypic material is deposited in BR and PC. The specimen in PC is large and has intact sporophytes. It is designated as the lectotype.

Original material of *Lepidopilidium theriorii* is deposited in BR, JE, and PC. A particularly large specimen in BR is designated as the lectotype.

Lepidopilidium subdevexum var. *intermedium* was described from a collection made by Tisserant in what is present-day Central African Republic. Duplicates of original material are deposited in BR and PC. The larger of the duplicates in PC is designated as the lectotype.

Discussion. Most specimens of *Lepidopilidium furcatum* form loosely complanate mats with frequently branched stems, although some specimens form dense tufts of erect branches. Elizabeth Britton's notes on the specimen packet of the lectotype of *L. furcatum* (NY) call attention to the mixture of these two unlike growth forms. The lateral leaves in both are similarly oblong-lanceolate and have narrowly long-acuminate apices. The sporophytes of *L. furcatum* have short setae and obloid capsules. Both the length and the ornamentation of the setae vary between specimens. The types of *L. hanningtonii* and *L. theriotii* have nearly smooth setae throughout, whereas the type of *L. attenuatum* has setae that are smooth below and lightly papillose above.

As noted by De Sloover (1975), sterile specimens of *Lepidopilidium furcatum* are exceedingly difficult to separate from *Lepidopilum lastii* Mitt. Both species are similar in their complanate-foliate habit, size, and leaf shape, although *L. lastii* tends to be slightly larger and have longer, less densely branched stems. Sterile specimens of *Lepidopilidium furcatum* can also be confused with *Thamniopsis pappeana* (Hampe) W. R. Buck. Ochyra and Pócs's (1992) *Bryophyta Africana Selecta* specimens No. *93*, as *Lepidopilidium han-*

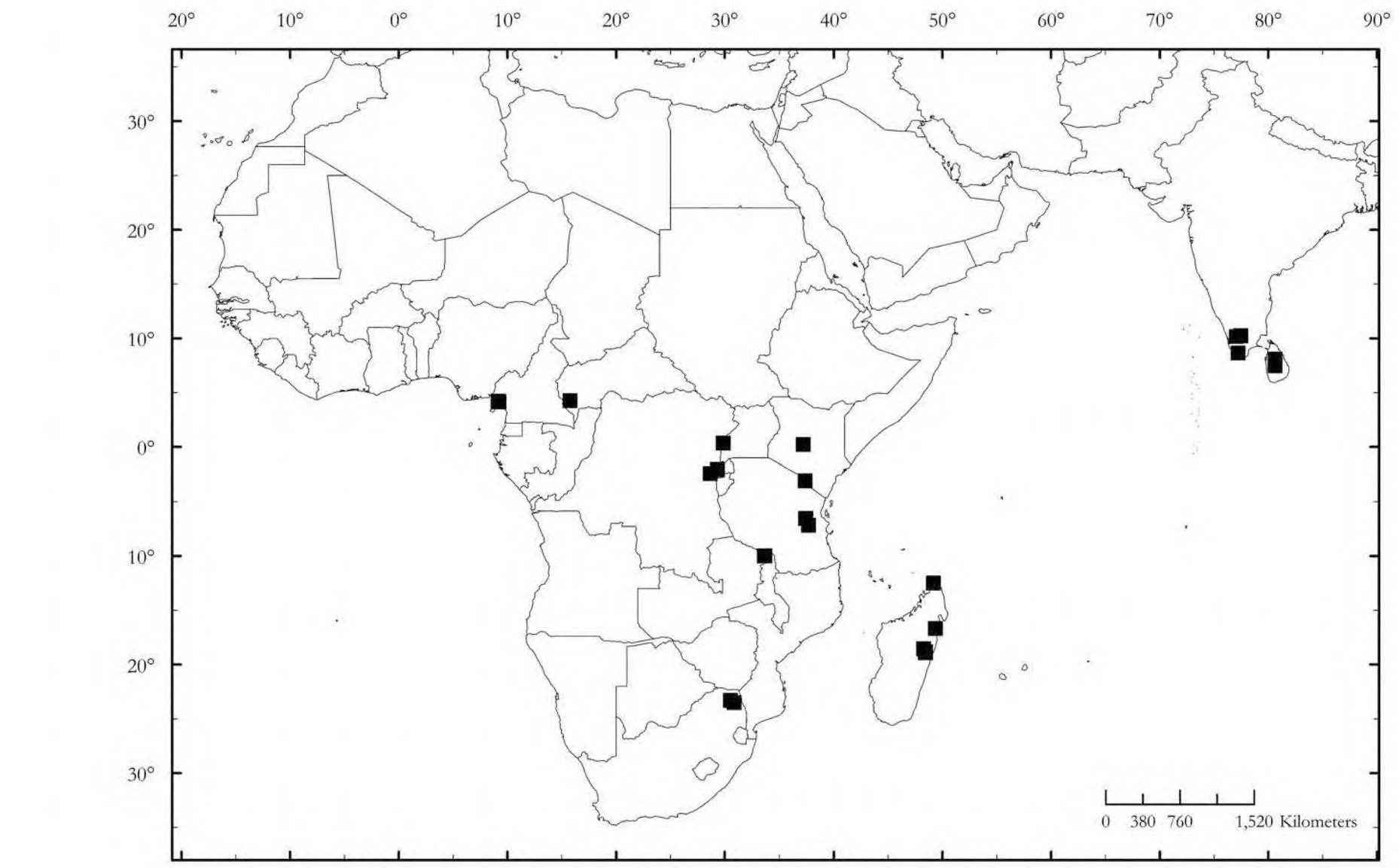


Figure 6. Distributions of *Lepidopilidium* species. —A. *Lepidopilidium furcatum* (Thwaites & Mitt.) Broth. (■). —B. *Lepidopilidium nitens* (Hornsch.) Broth. (●).

ningtonii, and residual specimens distributed from Foreau's *Musci Madurenses Indiae Meridionalis Exsiccati*, as *Lepidopilidium furcatum*, belong to *T. pappeana*. *Lepidopilidium furcatum* and *T. pappeana* are superficially similar, but differ in that *T. pappeana* has inflated, bifurcate teeth on the leaf margins.

Additional specimens examined. CAMEROON. **Southwest:** supra Buea, *Bornmüller 8* (NY); 1891, *Junger s.n.* (H). DEMOCRATIC REPUBLIC OF THE CONGO. **Sud Kivu:** *De Sloover 12913* (BR, MO), *12920* (BM, MO), *12941B* (BR, MO). KENYA. **Central:** Mt. Kenya Natl. Forest, S slopes of Mt. Kenya, above Castle Forest Station, *Crosby & Crosby 8732* (MO). MADAGASCAR. **Antsiranana:** Parc Natl. Montagne d'Ambre, *Touw & Snoek 25108* (L). **Toamasina:** Tamatave, 3 km SE of Perinet, *Crosby 14434* (MO); valley of Marimbona River, W of Soanierano, *Lam & Meeuse 5929A* (L); Périnet Réserve Forestiere at Andsibe, *Magill et al. 9616* (MO), *9636* (MO). MALAWI. July 1896, *Whyte s.n.* (H). RWANDA. **Cyangugu:** Uwinka, forêt de Rugege, rivière Buruli, *De Sloover 18839* (MO, NY, S). SOUTH AFRICA. **Transvaal:** *Crosby & Crosby 7612* (MO); *7617* (MO); *7662* (MO). TANZANIA. **Morogoro:** *Crosby et al. 8668* (BR, L, MO), *8669* (MO), *8679* (MO, L), *8689* (MO), *8693* (MO), *8700* (MO), *8704* (MO), *14437* (MO); *Pócs et al. 6220/D* (MO). **Ulanga:** Sanje, *Thomas 3762A* (NY).

INDIA. **Tamil Nadu:** Madras State, Madura Distr., Palni Hills, Kodaikanal, 1929, *Foreau s.n.* (US); *Daniels & Kariyappa 3627 p.p.* (MO). SRI LANKA. **Central:** Feb. 2006, *Herzog s.n.* (H), *Herzog 47/a* (JE); *Naylor Beckett C169* (H). **North Central:** Ritigala, *Naylor Beckett 89* (NY).

5. **Lepidopilidium isleanum** (Besch.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3, II): 944. 1907. Basionym: *Lepidopilum isleanum* Besch., Ann. Sci. Nat., Bot., sér. 6, 10: 279. 1880. TYPE CITATION: La Réunion: entre les branches de Calamagrostis (?) Belous, 25 mai 1874, *G. de l'Isle* no. *183*. TYPE: La Réunion. *G. de l'Isle 183* (lectotype, designated here, BM!; isotypes, NY!, S!). Figure 7.

Lepidopilum flexuosum Besch., Ann. Sci. Nat., Bot., sér. 6, 10: 280. 1880, syn. nov. *Lepidopilidium flexuosum* (Besch.) Broth. ex Paris, Coll. Nom. Broth. 17. 1909. TYPE CITATION: La Réunion: plaine des Palmistes, *G. de l'Isle*, no. *293*. Rare. TYPE: La Réunion. Plaine des Palmistes, *G. de l'Isle 293* (lectotype, designated here, BM!; isotype, NY!).

Lepidopilidium parvulum Schimp. ex Cardot, in C. H. Wright ex Cardot, in Grandidier, Hist. Phys. Madagascar, Mousses 414. 1915, syn. nov. *Lepidopilum parvulum* Schimp., in C. H. Wright, J. Bot. 26: 266. 1888, nom. inval. [lacks description]. TYPE CITATION: Madagascar. (Nord-Ouest), sans indication de localité (*Pervillé*: herb. Jard. Bot. Kew). TYPE: Madagascar. s. loc. *Pervillé M. par. 52* (lectotype, designated here, BM!; isolectotype, NY!).

Lepidopilum subrevolutum Renauld & Cardot, in Renauld, Suppl. Prodr. Fl. Bryol. Madagascar 20: 80, tab. 20, fig. 2. 1909, syn. nov. *Lepidopilidium subrevolutum* (Renauld & Cardot) Cardot, in Grandidier, Hist. Phys. Madagascar, Mousses 414. 1915, tab. 97A, fig. 3a–e. TYPE CITATION: Madagascar. forêt de Analamazaotra, Rev. *Camboué*, 1890. TYPE: Madagascar. *P. Camboué s.n.* (lectotype, designated here, PC!; isotype, PC!).

Plants glossy, pale green to golden-yellow, sometimes tinted red, in dense mats; stems prostrate, to 3 cm, sparsely branched, complanate-foliate. Leaves not or slightly dimorphic, contorted when dry; dorsal and ventral leaves symmetric, mostly ovate to oblong-ovate, 1.6–2.5 × 0.7–1 mm, abruptly short-acuminate; lateral leaves slightly asymmetric, oblong-ovate or oblong, 1.8–3 × 0.6–1.1 mm, abruptly acuminate with short, slender tips, rounded to the insertion; margins serrulate to serrate above, becoming serrulate to entire below, plane or narrowly recurved, obscurely bordered by 1 or 2 rows of narrow, elongate cells, confluent at apices; costae extending to midleaf, diverging throughout, uneven, not projecting at apices; laminal cells smooth, thick-walled, sometimes porose, apical and median cells oval-hexagonal to narrowly or broadly rhomboidal, 40–72 × 18–22 μm, becoming elongate-rhomboidal below, basal cells enlarged, rectangular. Gemmae present. Plants autoicous. Setae flexuous, 7–15 mm, yellow to red, lightly papillose below to smooth, lightly or densely papillose above, sometimes smooth; capsules suberect to inclined, sometimes horizontal, obloid to obloid-cylindric, 1.3–2 mm long, sometimes curved, often constricted below the mouth; opercula conic-rostrate, 1 mm long. Spores 25–32 μm, yellow, finely papillose. Calyptrae 2–2.5 mm long.

Iconography. Renauld (1909: tab. 20, fig. 2a–e, as *Lepidopilum subrevolutum* Renauld & Cardot): Renauld & Cardot (1915: tab. 97A, fig. 3a–e, as *Lepidopilum subrevolutum* Renauld & Cardot).

Habitat and distribution. *Lepidopilidium isleanum* is known from the type collections and a few additional specimens from Madagascar and La Réunion, where it has been collected on wet rocks, logs, and tree trunks and branches at 1500–1965 m elevation (Fig. 2A).

Nomenclatural notes. *Lepidopilum isleanum* and *L. flexuosum* were described simultaneously by Bescherelle (1880) from two of de l'Isle's specimens (*183* and *293*, respectively) that were collected on the island of La Réunion. Syntypic material of each species is deposited in Bescherelle's herbarium, now in BM. These are designated as lectotypes.

The type of *Lepidopilidium parvulum* was described from specimens collected by Pervillé in Madagascar. Two specimens matching the type citation were found in BM, neither of which are annotated by Cardot. Although no collection number was cited in the protologue, both BM specimens have numbers (*Pervillé*

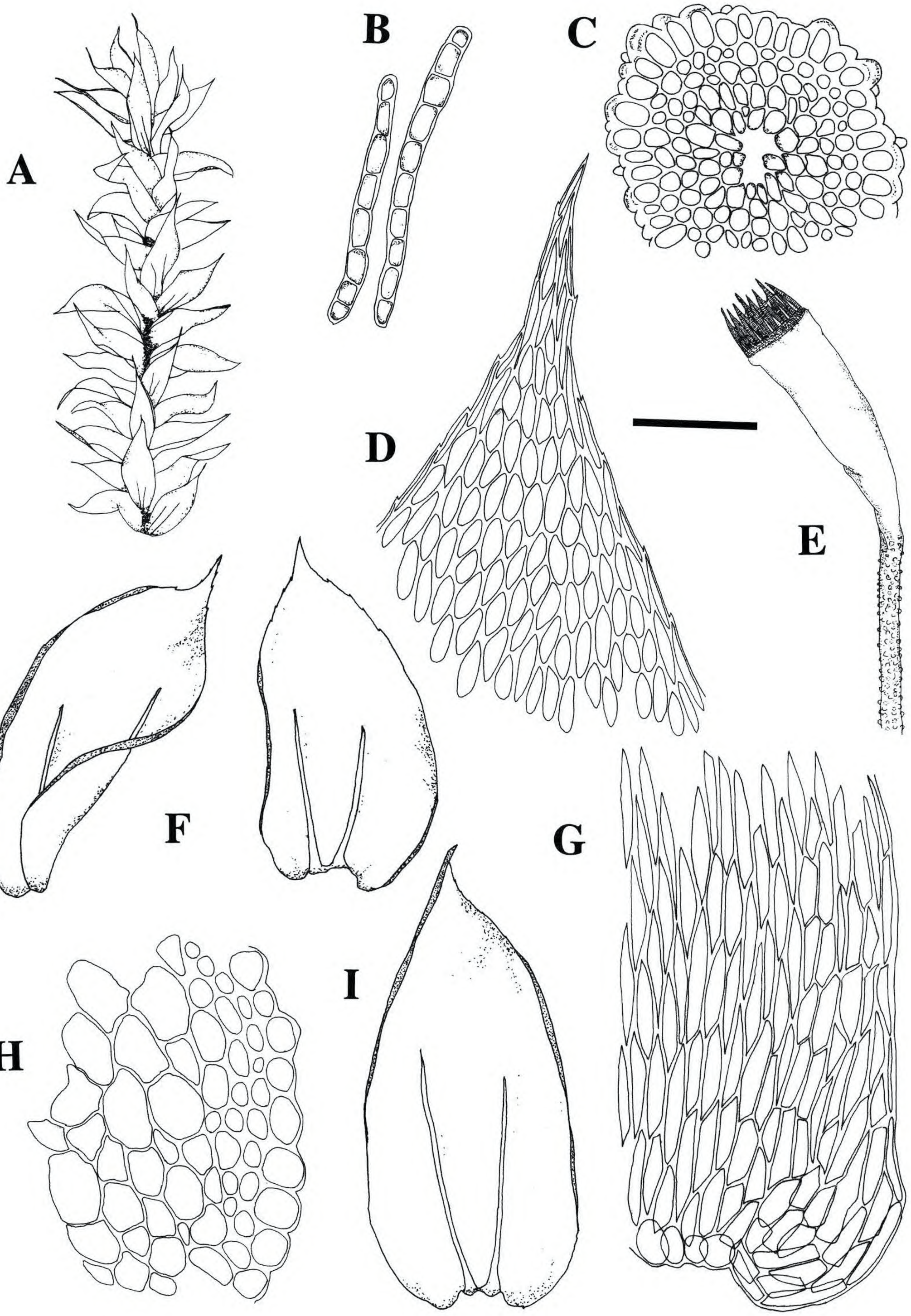


Figure 7. *Lepidopilidium isleanum* (Besch.) Broth. —A. Habit. —B. Gemmae. —C. Transverse section of seta. —D. Lateral leaf apex. —E. Sporophyte. —F. Lateral leaves. —G. Basal laminal cells of lateral leaf. —H. Transverse section of stem. —I. Dorsal leaf. Scale bars: A = 1.96 mm; B, D, G = 0.13 mm; C, H = 0.06 mm; E = 0.8 mm; F, I = 0.6 mm. A drawn from *Carter 8057* (NY); B, D, F–I drawn from *Arts RÉU59/29* (BR); C, E drawn from syntype *Perville 41* (BM).

41 and *Pervillé M. par. 52*, respectively). Except for their setae ornamentation, the specimens appear to be morphologically identical. *Pervillé 41* has setae that are smooth below and densely papillose above, whereas specimen *Pervillé M. par. 52* has setae that are smooth below and mostly smooth above, with a few low, scattered papillae. The original description of *L. parvulum* notes the setae ornamentation to be smooth throughout. Since *Pervillé M. par. 52* more closely matches the setae ornamentation noted in the type description, it is considered to be the more appropriate specimen as lectotype.

Renauld and Cardot (1909) described *Lepidopilum subrevolutum* based on an unnumbered Malagasy collection made by Camboué in 1890. Three duplicates of original, syntypic material are deposited in PC. The largest of these is designated the lectotpye.

Discussion. *Lepidopilidium isleanum* has slightly asymmetrical, oblong-ovate to oblong lateral leaves that are rounded to the insertion. The leaves have oval-hexagonal to narrowly or broadly rhomboidal median cells, and are often bordered by one or two rows of narrowly elongate cells, best visible in the slender, abruptly short-acuminate apices. Perhaps the most noteworthy character of *L. isleanum* is its elongate (7–15 mm), flexuous setae.

Bescherelle (1880) described *Lepidopilum isleanum* alongside the name *L. flexuosum* for two specimens collected on La Réunion by de l'Isle. The setae of *L. isleanum* [≡ *Lepidopilidium isleanum*] were described as smooth below and smooth to lightly papillose above, whereas the setae of *L. flexuosum* [≡ *Lepidopilidium flexuosum*] were described as smooth to papillose below and densely papillose above.

Similarly, Renauld and Cardot (1915) treated two morphologically similar *Lepidopilidium* names from Madagascar, *L. subrevolutum* and *L. parvulum*, which differ only in their setae ornamentation as well. Renauld and Cardot's (1915) illustrations of *L. subrevolutum* (as *Lepidopilum subrevolutum*) depict the densely papillose setae. On the other hand, *L. parvulum*, which was originally described as having smooth setae, has some setae with distally scattered papillae. An examination of additional specimens from Madagascar and La Réunion found setae with variably scattered papillae as well, i.e., *Carter et al. 8057* (NY) and *Arts RÉU59/29* (BR). Although only a limited number of specimens, including types, were available for study, the setae ornamentation differences noted in the original descriptions are considered to be extremes in a continuum.

Additional specimens examined. LA RÉUNION. Cilaos, Cirque de Cilaos, *Carter et al. 7952* (NY), *8055* (NY), *8057* (NY), *Arts RÉU59/29* (BR); Salazie, Cirque de Salazie, *Carter 7952* (NY), *Arts RÉU07/31* (BR). MADAGASCAR. *Pervillé 41* (syntype, *Lepidopilidium parvulum*, BM!). **Fianarantsoa:** *Onraedt 71.m.5405* (BR).

6. **Lepidopilidium nitens** (Hornsch.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. Basionym: *Hookeria nitens* Hornsch., Fl. Bras. 1(2): 65. 1840. TYPE CITATION: Ad truncos putridos silvarum umbrosarum prope Novo-Friburgum in societate *Lepidopili subnervis*; Decembri, c. fr. maturis, *Beyrich*. TYPE: Brasilia prope Novo Friburgum, *Beyrich s.n.* (lectotype, designated here, BM [barcode BM000862091]!; isotype, BM!). Figure 8.

Plagiothecium regnellii Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(4): 44. 1876, syn. nov. *Lepidopilidium regnellii* (Ångstr.) W. R. Buck & Ireland, Fl. Neotrop. Monogr. 50: 19. 1989. TYPE CITATION: Brazil. Caldas, *Regnell 15* transmisit. TYPE: Brazil. Caldas, *A. F. Regnell 15* (lectotype, designated by Buck & Ireland, 1989: 19, S!; isolectotype, S!).

Lepidopilum laevisetum Hampe, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn ser. 4, 1: 124. 1879, syn. nov. *Lepidopilidium laevisetum* (Hampe) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: [Brazil.] Prope Rio de Janeiro: *Glaziou* (*9235*, *parce*) TYPE: [Brazil.] Rio de Janeiro, *Glaziou 9235* (lectotype, designated here, BM!; isotypes, BM!, BR!, G!, PC not seen).

Hookeria aureopurpurea Geh. & Hampe, Flora 64: 409. 1881, as "aureo-purpurea," syn. nov. *Lepidopilidium aureopurpureum* (Geh. & Hampe) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: [Brazil.] Prope Apiahy, Junio 1879, *Puiggari* (*179*, *192*). TYPE: Brazil. "Brasilia: prope Apiahy, S. Paulo," 1879, *G. L. T. Puiggari s.n.* (lectotype, designated here, BM [barcode BM000862101]!).

Hookeria subnitens Geh. & Hampe, Flora 64: 409. 1881. *Lepidopilidium subnitens* (Geh. & Hampe) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: [Brazil.] Prope Apiahy, Aprili–Mayo 1879, *Puiggari*; prope Iporanga, statu sterili, foliis serrate-dentatis: idem. TYPE: [Brazil.] "Brasilia prope Apiahy, S. Paulo," 1879, *G. L. T. Puiggari* s.n. (lectotype, designated here, BM [barcode BM000862089]!).

Hookeria subnitens var. *latior* Geh. & Hampe, Flora 64: 409. 1881, syn. nov. TYPE CITATION: [Brazil.] Prope Apiahy, Majo 1879, *Puiggari* (*538*). TYPE: Brazil, São Paulo, May 1879, *Puiggari 538* (lectotype, designated here, BM!).

Lepidopilum mariei Besch. ex Kindb., Enum. Bryin. Exot., suppl. 2, 100. 1891, nom. inval. [lacks description]. TYPE: Guadeloupe, *Marie 145* (type, NY!).

Hookeria entodontella Müll. Hal. ex Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21. 3(3): 40. 1895, syn. nov. *Hookeria entodontella* Müll. Hal., Hedwigia 39: 279. 1900, nom. illeg. *Lepidopilidium entodontella* (Müll. Hal. ex Broth.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: [Brazil.] Prov. S. Paulo, Santos, Sororocaba, in

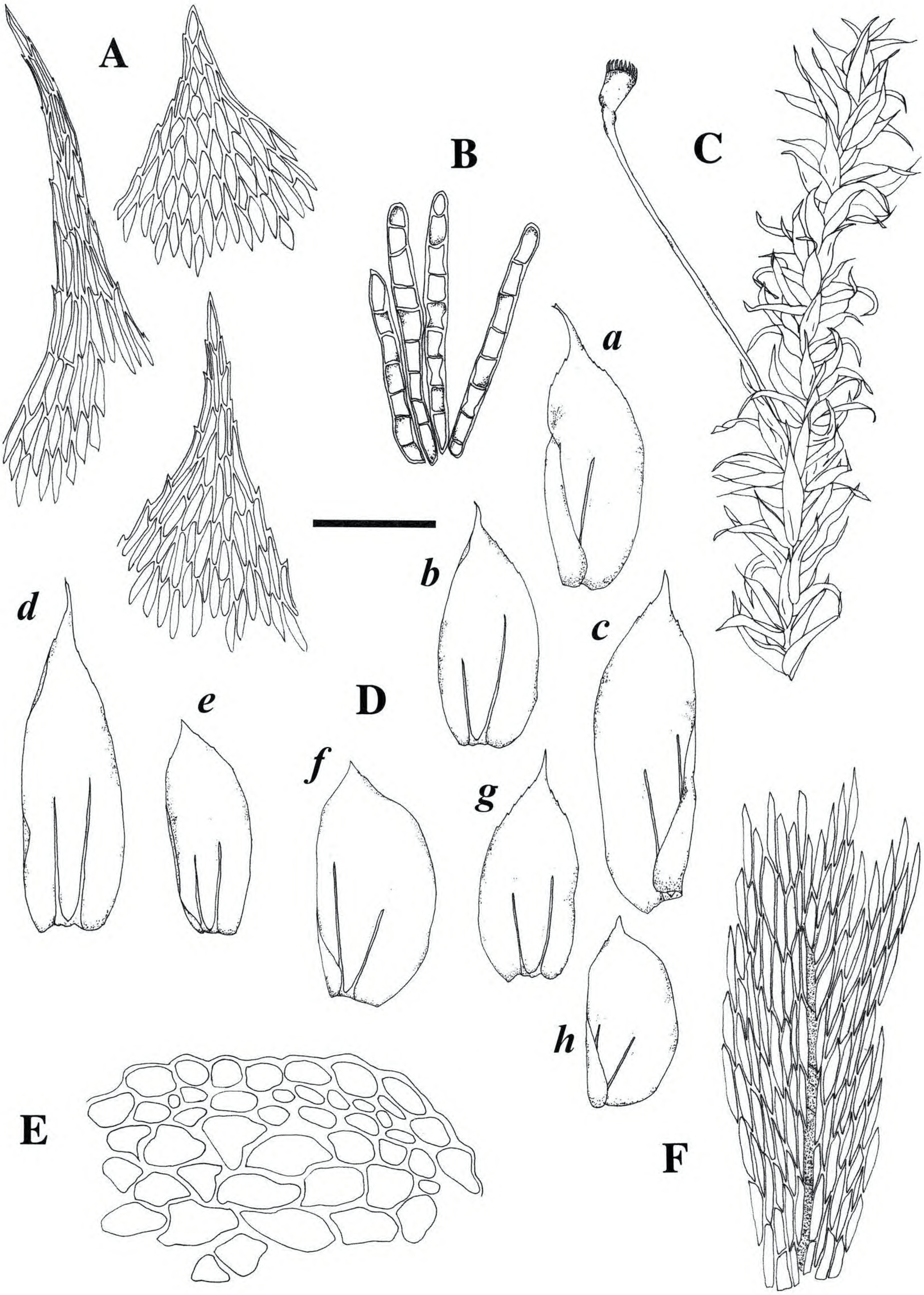


Figure 8. *Lepidopilidium nitens* (Hornsch.) Broth. —A. Lateral leaf apices. —B. Gemmae. —C. Habit with sporophyte. —D. Lateral leaves (*a–h*). —E. Transverse section of stem. —F. Median laminal cells of lateral leaf. Scale bars: A, B, F = 0.13 mm; C = 1.96 mm; D = 0.6 mm; E = 0.06 mm. A drawn from *Steyermark 103395* (MO); B, C, D*b*, E, F, drawn from lectotype, *Ule 1470* (S); D*a* drawn from *Richards 309* (U); D*c* drawn from *Elliott 206a* (BM); D*d* drawn from *Hoehne 122* (JE); D*e* drawn from *Glaziou 7090* (BM); D*f* drawn from *Britton 6581* (NY); D*g* drawn from *Allen 15115* (MO); D*h* drawn from lectotype, *Regnell 15* (S).

adscensu montis Morro de Curupira, 500 m (*Mosén n. 72*). TYPE: [Brazil.] "S[ão] Paulo, Santos, Sororocaba, in adscensu montis Morro de Curupira," 500 m, 30 Mar. 1875, *Mosén 72* (lectotype, designated here, S [barcode S-B121809]!; isotypes, H!, S!).

Crossomitrium portoricense Müll. Hal., Hedwigia 37: 244. 1898, as "Portoricense," syn. nov. *Lepidopilum portoricense* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 956. 1907. *Lepidopilidium portoricense* (Müll. Hal.) H. A. Crum & Steere, Bryologist 59: 253. 1956. TYPE CITATION: Portorico, prope Aybonito, ad arbores sylvae primaevae montis Cuyon, Nov. 1885, *P. Sintenis* in Hb. Krug et Urban. TYPE: [Puerto Rico.] "prope Aybonito, *P. Sintenis*" *Plantae Portoricenses*. F62, Aybonito, 3 Nov. 1885 (lectotype, designated here, BM!, isotypes, G!, NY!, S!).

Hookeria longicuspis Müll. Hal., Hedwigia 39: 273. 1900. *Lepidopilum longicuspis* Müll. Hal., in Ule, Hedwigia 38 (Beibl.): 59. 1899, nom. inval. [lacks description]. *Lepidopilidium longicuspis* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Brasilia, Sa. Catharina, Nova Venezia, ad truncos arborum sylvestrium, Julio 1891, *E. Ule*, Coll. No. *1030*. TYPE: [Brazil.] Santa Catarina, "Nova Venezia, ad truncos silvae," July 1891, *E. Ule s.n.* (lectotype, designated here, G!; isotypes, BM!, BR!, G!, JE!, L!, M!).

Hookeria tenuiseta Müll. Hal., Hedwigia 39: 272. 1900. *Lepidopilidium tenuisetum* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Brasilia, Sa. Catharina, colonia Blumenau, ad trunculum arboris sylvestris prope rivulum Mulde, Julio 1888, *E. Ule*, Coll. No. *317*; Joinville, in sylva primaeva, Junio 1888, sterilis: idem, No. *468*. TYPE: [Brazil.] "Brasilia, Blumenau, an einem Stämmchen im Walde an der Mulde," July 1888, *E. Ule 317* (lectotype, designated here, H!).

Hookeria gracilifrons Müll. Hal., Hedwigia 39: 279. 1900. syn. nov. *Lepidopilidium gracilifrons* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Brasilia, Minas Geraës, Ouro Preto, ad truncos arborum, Martio 1892, *E. Ule*, Coll. No. *1470*. TYPE: Brazil. "Brasilia, Minas Gerais: Ouro Preto," 1892, *E. Ule 1470* (lectotype, designated here, S!; isotype, US!).

Hookeria wainioi Broth., Acta Soc. Sci. Fenn. 19(5): 19. 1901, syn. nov. *Lepidopilidium wainioi* (Broth.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Minas Gerais, Caraça; planta mascula [*E. Wainio*]. TYPE: Brazil. "Brasilia, Minas Geraës, Caraça," 1885, *E. Wainio s.n.* (lectotype, designated here, S!).

Plants glossy, green to golden-yellow, sometimes tinted red, in dense to lax mats; stems prostrate, to 7 cm, irregularly branched, moderately to strongly complanate-foliate. Leaves evenly or densely spaced, strongly dimorphic; dorsal and ventral leaves appressed or erect-spreading when dry or wet, symmetric, elliptical, ovate, oblong-ovate, ovate-lanceolate, or oblong, 1–2.5 × 0.3–0.8 mm, abruptly acute, short-acuminate, or broadly acuminate; lateral leaves flat or shallowly concave, erect-spreading to falcate-spreading when dry, erect-spreading to wide-spreading, sometimes flexuous when wet; polymorphic: asymmetric, ovate, 1–1.3 × 0.5–0.6 mm, abruptly acute; or symmetric to asymmetric, oblong-ovate to oblong, 1.1–1.9 × 0.3–0.6 mm, acute to abruptly short-acuminate; or symmetric, oblong to oblong-lanceolate, 1.7–2.1 × 0.5–0.7 mm, narrowly long-acuminate; or symmetric, oblong-lanceolate, 2–2.6 × 0.4–0.7 mm, broadly long-acuminate; margins entire, serrulate, or serrate above, serrulate to entire below, plane or narrowly recurved, sometimes broadly incurved on one side at base, not or narrowly bordered by one or two rows of long, narrow cells; costae extending below, to, or above midleaf, parallel or diverging throughout, uneven, smooth at back, not projecting or weakly projecting at tips; laminal cells smooth, thin-walled, sometimes porose; apical and median cells hexagonal, rhomboidal, elongate-rhomboidal, or narrowly to broadly fusiform, 40–100 × 10–20 μm, becoming longer and narrow below; basal cells enlarged, short to long-rectangular. Gemmae present. Plants dioicous. Setae straight, 7–15 mm long, red-orange, smooth or sometimes lightly papillose above; capsules suberect to inclined, obloid-cylindric, 1.2–1.8 mm long, neck well-developed; opercula long conic-rostrate, 1 mm long. Spores 15–25 μm, yellow, finely papillose. Calyptrae 1.6–2 mm long.

Iconography. Welch (1969: 120, figs. 164–168, as *Lepidopilidium portoricense* (Müll. Hal.) H. A. Crum & Steere); Sehnem (1979: 77, tab. IX, fig. a, 1–7, as *L. gracilifrons* (Müll. Hal.) Broth.; fig. c, 1–5, as *L. laevisetum* (Hampe) Broth.); Florschütz-de Waard (1986: 332, fig. 130, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere); Bowers (1994: 818, fig. 616, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere); Duarte Bello (1997: 623, tab. 249, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere); Buck (1998: 44, tab. 16, figs. 1–8, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere; 2003: 100, fig. 91, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere); Peralta & Yano (2006: 59, fig. 7g–k, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere); Yano and Pôrto (2006: 18, figs. 9–12, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere); Vaz and Costa (2006: 979, figs. 7–14, as *L. brevisetum* (Hampe) Broth.; 979, figs. 15–20, as *L. laevisetum* (Hampe) Broth.); Vaz-Imbassahy and Costa (2008: 562, figs. 96–103, as *L. brevisetum* (Hampe) Broth.; 562, figs. 104–109, as *L. laevisetum* (Hampe) Broth.); Allen (2010: 547, fig. 186, as *L. portoricense* (Müll. Hal.) H. A. Crum & Steere).

Habitat and distribution. *Lepidopilidium nitens* is a widespread Neotropical species present in southern Mexico, Central America, the Caribbean, northern South America, and Brazil. It is an epiphyte noted as

collected from tree roots, bases, trunks, and branches, and branchlets as well as treelets, low shrubs, and lianas. The species is also epiphyllous. It occasionally occurs on decaying logs, stumps, and rocks at 420–1600 m elevation (Fig. 6B).

Nomenclatural notes. *Hookeria nitens* is the oldest name now placed in *Lepidopilidium*. The species was described from a collection made by Beyrich in Brazil. Three specimens of original, syntypic material are in BM, mounted on a single herbarium sheet alongside a non-typic Glaziou specimen (*7090*). The herbarium sheet also includes notes by Hampe concerning *Hookeria* sect. *Lamprophyllum*. The specimen bearing the label "ex herb. Hornschuch" is selected as the lectotype.

Hampe (1879) described *Lepidopilum laevisetum* based on the specimen *Glaziou 9235* from Rio de Janeiro, Brazil. Original material now resides in BM, BR, G, and PC, and each specimen has an original label with "Rio Janeiro" and "Glaziou" stamped on the bottom. Across the top of these labels is the name "Lepidopilum laevisetum," somewhat illegibly written in Hampe's handwriting. On specimens in BM and BR, the epithet "laevisetum" has been misread and reprinted on the herbarium sheet as "brevisetum," although the enclosed specimens do not match the type of *Lepidopilidium brevisetum*. The specimen *Glaziou 2935* in PC has a numbering error on the label that is incorrectly rewritten for *Glaziou 9235*. The specimen in Hampe's herbarium in BM is large and therefore designated as the lectotype.

The type citation for *Hookeria aureopurpurea* includes Puiggari's collection numbers *179* and *192*, although neither of these numbers were found during this study despite two attempts at locating them. However, an unnumbered specimen of *H. aureopurpurea*, annotated as "sp. nov." and marked as from Geheeb's herbarium as well as from Hampe's herbarium, now in BM, is original material. That specimen is designated as the lectotype.

Hookeria subnitens was described by Geheeb and Hampe (1881) from specimens collected by Puiggari in 1879 near Apiahy and Iporanga, Brazil. An unnumbered Puiggari specimen in BM noted from Geheeb's herbarium (as well as from Hampe's herbarium) is annotated as "sp. nov." and matches the type citation for the Apiahy locality except for the months of collection specified in the protologue as "Aprili–Majo 1879." Puiggari specimens in JE, L, and S have these months of collection on their labels but have the collection number *540* associated with them. Similarly, specimens in BM, H, and JE match the protologue information for the Iporanga locality but have the collection number *929* associated with them. No collection numbers are cited in the protologue. The specimen from Geheeb's herbarium in BM is selected as the lectotype.

Geheeb and Hampe (1881) described *Hookeria subnitens* var. *latior* from the specimen *Puiggari 538*, collected in May 1879 near Apiahy, Brazil. The single specimen is deposited in BM and marked as "Herb. Hampe–1881" and "ex Hb. Geheeb." No additional duplicates were discovered. This specimen is likely to be the only one used in the description of the new variety and is selected as the lectotype.

Original material of *Hookeria entodontella* is deposited in H as well as in S with duplicates. The collection in H is small, whereas those in S are large. The largest of these is designated as the lectotype.

Crossomitrium portoricense was described from a specimen collected in Puerto Rico by Sintensis in November 1885. The type citation notes the specimen to be deposited in the herbarium of Wilhelm and Urban, which was destroyed in World War II. Original material in BM, G, NY, and S mostly agrees with the specimen information cited in the protologue by Müller except for having "Hb. Krug et Urban" noted on the labels. Most of these specimens are small, but the BM specimen is large. It is designated as the lectotype.

Exsiccatal specimen No. *172* in Ule's (1899) *Bryotheca Brasiliensis* is original material of *Hookeria* (*Lepidopilidium*) *longicuspis* that was considered by Müller (1900). Although the collection number, *1030*, is not cited on any of the specimen labels in BM, BR, G, JE, L, and M, the label information matches the locality data from the protologue, including the date. Since Ule's herbarium was deposited in B, the duplicate bearing the *1030* collection number was likely destroyed during the 1 March 1943 bombing of Berlin (Merrill, 1943). A particularly large specimen with numerous sporophytes in G is designated as the lectotype.

Hookeria (*Lepidopilidium*) *tenuiseta* is based on two syntypic specimens collected by Ule (*317* and *468*). Only specimen *Ule 317* was located for this study, and it is designated as the lectotype.

Müller (1900) described *Hookeria gracilifrons* based on the specimen *Ule 1470*, collected from Minas Gerais, Brazil, in March 1892. The specimen deposited in Müller's herbarium at B was destroyed, but duplicates were located in S and US. The specimen in S is larger than the one in US and is designated as the lectotype.

Brotherus described *Hookeria wainioi* from an unnumbered specimen collected in 1885 by Wainio from Minas Gerais, Brazil. Original material is deposited in S, but no material of the type collection was located in Brotherus's herbarium in H. The specimen in S is designated as the lectotype.

Discussion. *Lepidopilidium nitens* has prostrate, moderately to strongly complanate-foliate stems; uniseriate, multicellular gemmae; dioicous sexuality; elongate, smooth to distally papillose setae; and suberect to inclined, obloid-cylindrical capsules. As seen from the list of conspecific synonyms, the species otherwise exhibits considerable plasticity, especially in its lateral leaves. In fact, the majority of the synonyms were originally described for differences in lateral leaf characters, such as color (*L. aureopurpureum* and *L. entodontella*), symmetry (*L. subnitens*), shape and size (*L. entodontella*, *L. laevisetum*, *L. regnellii*, *L. subnitens*, and *L. tenuisetum*), length of the apices (*L. gracilifrons* and *L. longicuspis*), serration of the margins (*L. laevisetum* and *L. wainioi*), length and ornamentation of the costae (*L. subnitens*), and the shape and size of the apical and median leaf cells (*L. gracilifrons* and *L. portoricense*). However, despite the large number of names, few of them were ever applied to specimens other than those for which they were described. Only the name *L. portoricense* has been widely used for specimens outside of a regional context, which is likely the result of it having been illustrated in several major floristic publications.

Brotherus (1924) was the first to recognize that *Lepidopilidium nitens* was polymorphic when he placed the names *L. longicuspis*, *L. subnitens*, and *L. tenuisetum* into synonymy. Although Brotherus also used names that are here considered synonymous to *L. nitens*, he no doubt encountered difficulties in applying them. For example, using strict type concepts, Brotherus assigned three different names to Schiffner's specimens from southeastern Brazil that are close in sequential collection numbers and have identical label information. The name *L. aureopurpureum* was used for No. *1833*; *L. gracilifrons* was given to No. *1834*; and *L. laevisetum* was used for No. *1847*. A re-examination of these three collections found intergradations in the symmetry and shape of the lateral leaves, length of the apices, serration of the upper leaf margins, length of the costae, and shape and length of the apical and median leaf cells. In fact, plants in the same collection, but inhabiting different parts of the substrate, were found to have morphological differences. In addition, lateral leaves examined from near the tips and ends of stems and branches were found to be morphologically dissimilar from those on older sections of the stem. Depending on which lateral leaves are used in making the determination, a single stem can be assigned to at least two different names.

In this revision, approximately 250 specimens of *Lepidopilidium nitens* were examined from throughout the range of the now synonymous names. Due to the observed variability within individual specimens as well as on individual stems none of the previously recognized names are considered tenable at any formal taxonomic rank. However, specimens do seem to correspond to three morphological expressions, albeit with some clinal tendencies.

Key to the Morphological Expressions of *Lepidopilidium nitens*

1a. Plants strongly complanate, stems mostly unbranched; lateral leaves strongly asymmetric and elliptical or ovate; apices acute to short-acuminate; margins entire or serrulate; upper leaf cells hexagonal to short-rhomboidal; costae ending at midleaf or below and not projecting at the tips ..... *L. regnellii* (Ångstr.) W. R. Buck & Ireland

1b. Plants complanate, frequently and irregularly branched; lateral leaves symmetrical or asymmetrical, variously ovate, oblong, or lanceolate; margins serrulate to serrate; upper leaf cells short to elongate-rhomboidal, or fusiform; costae ending at midleaf or above, sometimes projecting at the tips.

2a. Lateral leaves mostly asymmetrical, ovate or oblong; apices abruptly and narrowly short- to long-acuminate, the acumen reaching to 0.4 mm long; upper leaf cells short to elongate-rhomboidal; costae extending to midleaf ..... *L. nitens* (Hornsch.) Broth.

2b. Lateral leaves mostly symmetric or slightly asymmetric, oblong, lanceolate-oblong, or ovate-lanceolate; apices gradually acuminate, narrowing from midleaf; upper leaf cells fusiform; costae ending above midleaf, sometimes with a few weak teeth at back ..... *L. subnitens* (Geh. & Hampe) Broth.

The typical morphological expression of *Lepidopilidium nitens*, including the types of *L. gracilifrons*, *L. portoricense*, *L. tenuisetum*, and *L. wainioi*, has been illustrated in several regional treatments (Bowers, 1994; Buck, 1998; Peralta & Yano, 2006; Allen, 2010). Comparisons of these illustrations indicate some of the variability associated with the lateral leaf shape, length of the apices, leaf margin serration, and length of the costae. This phenotypic variability has been collected from the trunks, twigs, and leaves of trees and shrubs as well as on rotting logs and damp, shaded rocks. The plants are often tinted red, and have complanate, irregularly branched stems and evenly spaced leaves. The lateral leaves are asymmetrical, ovate or oblong, and somewhat concave. The length of the lateral leaf apices vary from abruptly and narrowly short- to long-acuminate, the acumen reaching up to 0.4 mm long. In addition, the leaves are sometimes bordered by a few narrowly elongate cells. The margins are serrate to serrulate above, rarely entire, and the

marginal teeth are occasionally and sporadically bifid, especially noticeable at the apical tips of specimens with long-acuminate apices. The costae extend to midleaf or slightly above and sometimes project at the tips. The apical and median cells are mostly short to elongate-rhomboidal but occasionally can be hexagonal in oblong-ovate leaves or elongate-fusiform in more oblong-lanceolate leaves.

The next morphological expression, centered on the name *Lepidopilidium regnellii*, is considered to be a colonizing growth form that occurs on rotting wood, bases of trees, and on moist, shaded rocks. It contains mostly unpigmented plants that are strongly flattened, have mostly unbranched stems, and bear numerous gemmae. In addition, the leaves are crowded, strongly asymmetric, elliptical or ovate, flat, and have acute to short-acuminate apices; the leaf margins are elimbate, mostly entire to serrulate; the costae are uneven, diverge, and end below midleaf; and the apical and median leaf cells are hexagonal to rhomboidal. Specimens with sporophytes have not been observed. This expression is difficult to separate from the scabrisetum group in *Lepidopilum*, based on *L. scabrisetum*.

At the opposite extreme of the *Lepidopilidium regnellii* expression for variability in *L. nitens* is a more robust and densely foliate expression that occurs on tree branches, twigs, and leaves. It includes the types of *L. aureopurpureum*, *L. entodontella*, *L. longicuspis*, and *L. subnitens*, and has been cited by several authors as *L. laevisetum* (Sehnem, 1979; Robinson, 1986; Buck et al., 2005; Vaz & Costa, 2006; Vaz-Imbassahy & Costa, 2008). The type of *L. laevisetum* (*Glaziou 9235*, BM) has asymmetrical, oblong to ovate leaves (1.4–2 × 0.7–9 mm), costae that do not project at the tips, and rhomboidal leaf cells (20–60 × 12–16 μm). It is a better match for the typical expression of *L. nitens* than the *subnitens* expression. Although *L. laevisetum* was originally described as autoicous, the type is in fact dioicous. The *subnitens* expression is yellow-green to golden in color and sometimes tinted red. The stems are complanate-foliate, frequently and irregularly branched, and have closely spaced, slightly shriveled leaves when dry. The lateral leaves are more or less symmetric, lanceolate to oblong-lanceolate, and have broadly to narrowly long-acuminate apices. Additionally, the leaf margins are serrate to sharply serrate with a few occasional bifid teeth; the costae extend to midleaf or above, are sometimes toothed at back, and often weakly to strongly project at the tips. Lastly, the apical and median leaf cells are mostly fusiform throughout.

Additional specimens examined. BELIZE. **Cayo:** Doyles's Delight, *Allen 15042* (MO), *15095* (MO), *15115* (MO), *15243* (MO); Maya Mtns. above Mukle Bal Tsul ruin, Bladen Nature Reserve, *Whittemore 6230* (MO). **Toledo:** Doyles's Delight, *Allen 15462* (MO), *15457* (MO), *15471B* (MO), *15486B* (MO), *15121* (MO), *15374* (MO), *15424* (MO), *15483* (MO); Columbia River Forest Reserve, *Allen 18826* (MO), *18898* (MO), *18930* (MO), *18950* (MO), *18951* (MO), *18955* (MO, NY), *19014* (MO), *Holst 4335* (MO); Middle Snake Creek basin, Bladen Nature Reserve, *Whittemore 6339* (MO). COSTA RICA. **Alajuela:** Santiago, San Ramón, 1901, *Brenes s.n.* (NY). **Cartago:** W bank of Río Grande de Orosi, above confluence with Río Villegas, *Crosby 8578* (MO). **Puntarenas:** Monteverde, *James 1969-80* (MO). **San José:** vic. Santa Mariá de Dota, *Standley 42431B* (FH, NY). HONDURAS. **Copán:** Copán Ruinas Mpio., *Allen 17729* (MO). NICARAGUA. **Nueva Segovia:** Cerro Mogotón, *Magill 14812* (MO).

CUBA. **Granma:** Falda Sierra Maestra, NE del Puntón del Mate, *Bucher 457* (FH, NY). **Santiago de Cuba:** La Gran Piedra, *Buck 7562* (NY); Loma del Gato, *Hioram 11951* (NY), *Leon et al. 10257* (NY); Loma San Juan, *Hioram 12703* (NY), *13702* (NY); Sevilla Estate, near Santiago, Jiquarito Mtn., Sierra Maestra, *Taylor 492* (NY). DOMINICA. **St. Andrew Parish:** Morne Diablotin, *Elliott 1068* (BM, FH, NY). **St. Joseph Parish:** Morne Couronne, *Elliott 206a* (BM, FH, NY). **St. Patrick Parish:** Morne Trois Pitons, *Elliott 2322* (BM, FH, NY). DOMINICAN REPUBLIC. **La Vega:** Loma Campana, *Allard 18633* (NY), *18778* (NY), *18780* (NY). REPUBLIC OF TRINIDAD AND TOBAGO. **Saint George County:** trail to Morne Bleu from summit of Arima-Blanchisseuse Rd., *Crosby 2110* (MO). PUERTO RICO. **Adjuntas:** Alto de la Bandera, *Britton & Marble 2212* (MO, NY). **Barranquitas:** Monte Torrecilla, *Britton et al. 5693* (NY); upper slopes of La Torrecilla, *Steere 4522* (MO, NY), *4543* (MO), *4562* (MO), *4563* (MO), *4565* (MO), *4567* (MO), *4571* (MO), *4585* (MO), *4645* (MO), *4631* (MO), *4633* (MO), *4906a* (MO). **Cayey:** Twin Mtn. betw. Cayey & Salinas, *Steere 5268* (MO, NY), *5269* (MO). **Guayama:** mtn. betw. Guayama & Cayey, *Britton et al. 6581* (NY). **Jayuua:** Toro Negro State Forest, *Griffin 325* (NY); Santa Rosa, *Pagán 314* (MO); Los Picachos de Jayuya, *Pagán 308* (MO), *311* (MO), *325* (MO); Serro de la Punta, *Steere 6168* (MO, NY); Toro Negro Reservoir, *Steere 6902* (MO, NY). **Lares:** Monte Torrecilla, July 1911, *Hioram s.n.* (NY). **Maricao:** Maricao to Monte Alegrillo, *Britton 2645* (MO, NY, S), *2647* (NY, S); Reserva Forestal Maricao, along Hwy. 120 at Km. 13.8, *Reese 14567* (MO); CCC trail number, *Steere 5555* (MO, NY); summit of high ridge, *Steere 5763* (MO), *5789* (MO), *5800* (MO). **Ponce:** Hac. San Narciso, *Britton & Britton 7308* (NY). **Rio Grande:** El Yunque Trail, *Grout & Steere 60* (NY), *67* (NY), *70* (NY). **Utuado:** Mt. Morales, near Utado, *Britton & Marble 1179* (NY).

BRAZIL. **Bahia:** Mpio. de Ilhéus, cidade de Ilhéus, Mata da Esperança, *Lisbôa de Oliveira 80* (NY). **Minas Gerais:** Caldas, s.d., *Regnell s.n.* (S). **Paraná:** Serra do Mar, Carvalho, *Dusén 8617* (FH, M, S); São José dos Pinhais, Serra do Emboque, *Hatschbach 19658* (NY); Quatro Barras, Morro Mãe Catira, *Kummrow 3049* (NY). **Rio de Janerio:** *Glaziou 7090 p.p.* (BM, NY, S); Corcovado, Dec. 1911, *Herzog s.n.* (JE, S), *12* (JE); *Mosén 157* (H, S); Natl. park Itatiaia bei Itatiaia, an schattigem Gestein im Regenwald beim Wasserfall Veu da Noiva, *Schäfer-Verwimp 9237* (NY); Petropolis, Araras, base da Pedra Maria Comprida, *Sucre 2552* (MO); Novo Friburgo, Feb. 1900, *Ule s.n.* (FH); Parque Nac. Itatiaia along trail to Véu de Noiva & Itaporani,

Vital & Buck 19980 (MO, NY, SP), *20025* (MO, NY). **Rio Grande do Sul:** São Francisco de Paula, Taimbé, *Sehnem 6879* (NY). **São Paulo:** *Hoehne 404* (JE); Apiahy, 1879, *Puiggari 540* (syntype, *Hookeria subnitens*, JE!, L!, S!); Apiahy, July 1880, *Puiggari s.n.* (JE); Apiahy, Aug. 1882, *Puiggari s.n.* (JE); prope Iporange, 1879, *Puiggari 929* (syntype, *Hookeria subnitens*, BM!, H!, JE!); Alto da Serra, *Hoehne 16/a* (JE); Alto da Serra, *Hoehne 37* (JE, M); Bosque da Saúde, *Hoehne s.n.* (M), *48* (JE), *56* (JE), *57* (JE), *64* (JE); Estrada do Vergueiro, *Hoehne 122* (JE, M, S); Estação Biol., Alto da Serra, *Hoehne 673* (JE); Tabapuã, *Hoehne 72* (JE, S), *91* (JE), *315* (JE), *382* (JE); Estação Biol., Alto da Serra, *Gehrt 506* (JE); Serra do Mar bei Paranapiacaba, zwischen São Paulo & Santos, *Schäfer-Verwimp & Verwimp 7141* (NY); prope Rio Grande ad São Paulo Railway, *Schiffner 512*, *688* (BM, M, S); Rio Mambu, Conceição de Itanhaen, *Schiffner 538* (S), *1430* (BM, M); Alto da Serra, *Schiffner 860* (BM, S), *1305* (BM); prope Barra Mansa, distr. Urbis Itapecirica, *Schiffner 1453* (BM); prope São Bernardo haud procul ab urbe São Paulo, *Schiffner 1833* (BM), *1834* (BM), *1847* (BM); Serra do Cayazique, prope Santos, *Schiffner 1856* (BM); Pindamonhagaba Co., ca. 2 km NE from Pico de Itapeva, *Vital DV-1940* (NY); Mpio. Juquitiba, *Vital 7143* (MO). FRENCH GUIANA. **Cayenne:** Sommet Tabulaire, *Cremers 6787* (U), *6791* (U). **Saint-Laurent-du-Maroni:** Canton de Maripasoula, *Buck 25571* (NY), *25572* (NY), *25582* (NY), *25622* (NY), *25637* (MO, NY), *25730* (NY), *25747* (NY), *25770* (NY), *25774* (NY); Montagne de l'Inini, *Onraedt 8979* (U), *8980* (U), *8990* (U), *8995* (U), *8996* (U), *9004* (U), *9059* (U), *9079* (U), *9082* (U), *9171* (U), *9227* (U), *9239* (U), *9245* (U), *9246* (U), *9249* (U), *9265* (U). **Saül:** Mont Galbao, *Buck 33253* (MO, NY), *33303* (NY), *Cremers 4049* (U), *4050* (U), *4098* (U), *4104* (U), *4149* (U), *6098* (U). GUYANA. **Cuyuni-Mazaruni:** upper Mazaruni River, Karowtipu Mtn., *Boom & Gopaul 7473* (NY); trail from Kamarang River to Pwipwi Mtn., *Gradstein 5717* (U). **Essequibo Islands-West Demerara:** Essequibo River, Moraballi Creek near Bartica, *Richards 309* (NY), *321* (NY, U). **Potaro-Siparuni:** Kaieteur Falls Natl. Park, *Newton 3422* (U); Paramakatoi, Para Mtn., *Newton 3534* (U), *3545* (U), *3551* (U). PARAGUAY. **Caazapá:** Estancia Golondrina, Reserva Privada Ypeti, *Zardini & Hellman 49038* (MO). SURINAME. **Brokopondo:** Brownsberg Massif, *Allen 19408* (MO); Brownsberg Nature Park, *Florschütz-de Waard & Florschütz 4622* (U), *4702* (U), *4722* (U), *4752* (U), *4759* (U), *Florschütz-de Waard & Zielman 5032* (U). **Sipaliwini:** Tafelberg, W rim of Arrowhead Basin, *Allen 23684* (MO), *23690* (MO, NY); Tafelberg, trail from Augustus Creek to North Ridge, *Allen 20578* (MO), *20630* (MO), *23339* (MO), *23348* (MO), *23363* (MO); Eilerts De Haan Gebergte, *Allen 25502* (U), *25528* (MO); Emmaketen, *BW 5655A* (U); Helling Ebbatop, van Asch van Wijcksgebergte, *Florschütz-de Waard & Florschütz 1486* (U), *1490* (U); Lely Mtns., *Florschütz-de Waard & Florschütz 4811* (U), *4871* (U), *Lindeman et al. 61b* (U), *506* (U); Bakhuis Mtns., in montibus Bakhuis inter flum. Kabalebo et Coppename Sinistrum, *Florschütz-de Waard & Maas 2870* (U), *2935* (U); Nassau Mtns., *Lindeman 7040* (U). VENEZUELA. **Aragua:** Parque Nac. Henri Pittier, bosque de Rancho Grande, *Agostini & Cobo 197* (MO, NY, U), *199* (MO); Distr. Girardot, Parque Nac. Henri Pittier (Rancho Grande), La Cumbre de Rancho Grande trail, *Davidse et al. 16667C* (MO), *16693* (MO); Parque Nac. Henri Pittier, Portachuelo, *Hokche et al. 810* (U), *Luteyn 8226* (U); Parque Nac. Henri Pittier, cumber Rancho Grande, *Morales 1737* (MO); Nebelwald von Rancho Grande, *Mägdefrau 350* (M), *372* (M, U); Maracay, Choroní, *Mägdefrau 476* (M, U), *487* (M, U), *497* (M); Rancho Grande, 17 Jan. 1971, *Ojasti s.n.* (MO, U). **Distrito Federal:** 6 km W of El Junquito on rd. betw. Caracas & Colonia Tovar, *Nee & Whalen 16865* (NY), *16868* (NY). **Falcón:** Sierra de San Luis, vía Coro-Uria, *Griffin & López-Figueiras PV-1614* (NY). **Lara:** Distr. Palavecino, selva dublada, Fila de Terepaima, entre el Alto de Chuparral y la Loma Redonda, *Steyermark et al. 103395* (FH, MO, U, US). **Miranda:** Parque Nac. Macarao, el junquito, *Morales 1441* (MO); Parque Nac. Guatopo, NE of hwy., 18 km NNW of Altagracia de Orituco, *Nee 17910* (NY), *17914* (NY), *17919* (NY), *17921* (NY), *17922* (NY); Cerros del Bachiller, *Steyermark & Davidse 116605* (MO), *116606* (MO), *116607* (MO), *116686* (MO), *116709A* (MO), *116838A* (MO). **Sucre:** Peninsula de Paria, Cerro de Río Arriba, *Steyermark & Rabe 96207* (US).

Excluded Taxa

Lepidopilum caudicaule Müll. Hal., Hedwigia 39: 272. 1900. *Lepidopilidium caudicaule* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1(3): 944. 1907. TYPE CITATION: Brasilia, Rio de Janeiro, Serra dos Orgãos, ad rupes Serrae, Dec. 1891, *E. Ule*, Coll. No. *1249*. TYPE: Brazil. Minas Gerais, Serra dos Orgaos, an Falsom in der Serra, Dec. 1891, [*E.*] *Ule 1249* (types, H!, US!).

Müller (1900) described *Lepidopilum caudicaule* based on Ule's specimen No. *1249*, which lacked sporophytes. Although the name was originally placed in *Lepidopilum*, Müller suggested *Lepidopilidium* as a possible alternative genus. The name has since been transferred to *Lepidopilidium* (Brotherus, 1907), although the original placement has also been maintained (Sehnem, 1979; Vaz & Costa, 2006; Vaz-Imbassahy & Costa, 2008). Sehnem (1979) based his decision to include *Lepidopilum caudicaule* in *Lepidopilum* on one of his own specimens that was gametophytically similar to the type description, was collected from a habitat similar to that cited in the protologue, and had sporophytes. Vaz-Imbassahy and Costa (2008) corroborated Sehnem's specimen with a type in R that they illustrate as having sporophytes, despite this being contrary to the type description. Type specimens in H and US lack sporophytes.

Lepidopilum pallidonitens (Müll. Hal.) Paris, Index Bryol. Suppl. 223. 1900. TYPE: Bolivia. Cochabamba, prope Choquecamata, June 1889, *Germain s.n.* (type, NY not seen).

Lepidopilum plebejum Müll. Hal., Hedwigia 39: 272. 1900. *Lepidopilidium plebejum* (Müll. Hal.) Sehnem, Pesquisas, Bot. 33: 32. 1979, syn. nov. TYPE CITATION: Brasilia, Sa. Catharina, Tubarão, in lingo putrido sylvestri, Oct. 1889, *E. Ule*, Coll. No. *768*; colonia Blumenau, ad truncum arboris sylvestris ad rivulum Ribeirão-fresco, Sep. 1888, idem, Coll. No. *473*. TYPE: [Brazil.] Estado de Santa Catarina. Num tronco no mato do Ribeirão-fresco perto de Blumenau. Sep.

1888, [*E.*] *Ule 473* (lectotype, designated here, PC!; isolectotype, H!).

Müller (1900) originally described *Lepidopilum plebejum* Müll. Hal. from two specimens that lacked sporophytes. A detailed description of the sporophyte was later provided by Sehnem (1979) based on his own specimen that had been collected in a habitat similar to that described in the protologue. Sehnem described the sporophytes as having distally papillose, 3-mm setae, with erect, 1-mm-long capsules and a hookeriaceous-type peristome. These characters led him to transfer *Lepidopilum plebejum* to *Lepidopilidium*. However, Sehnem's sporophyte description and specimen, *Sehnem 6491* (NY), belongs to *Lepidopilidium brevisteum*. Despite the lack of sporophytes in the type specimen, *Lepidopilum plebejum* is better placed in synonymy with *Lepidopilum pallidonitens* (Müll. Hal.) Paris. The specimen *Ule 473* is selected as the lectotype. It has strongly complanate, oblong-ovate, 2- to 3-mm-long leaves, broadly acuminate and apiculate apices, serrulate margins, and long-fusiform laminal cells that are shorter near the leaf apices and correspond to that of *L. pallidonitens*.

Hookeriopsis pallidifolia (Mitt.) Geh. & Herzog, Biblioth. Bot. 73: 59. 1910. *Hookeria pallidifolia* Mitt., in J. C. Melliss, St. Helena 362. 1875. *Lepidopilidium pallidifolium* (Mitt.) Vaz-Imbassahy & D. P. Costa, Nova Hedwigia 88: 467. 2009. TYPE CITATION: amongst the grass on the high land; a bright-green moss. *Dr. Hooker*, Melliss; also in *Herb. Turner* the specimen marked East Indies, *J. D.* (*Dickson*). TYPE: [United Kingdom, overseas territory]. St. Helena Island, s.d., *Hooker 427* (lectotype, designated by Vaz-Imbassahy & Costa, 2009: 467, NY!; isolectotype, BM!).

Mitten (1875) described *Hookeria pallidifolia* from a specimen collected by J. D. Hooker on St. Helena Island and another obtained by J. D. Dickson that was labeled East Indies. The original description, which was later repeated by Geheeb and Herzog (1910), remains the only detailed account of *H. pallidifolia*. The species is characterized as small, loosely tufted, and irregularly branched; having slightly asymmetrical and concave, oblong-lanceolate leaves; acute apices; inflexed, entire to crenulate margins; short and inconspicuously forked costae; narrowly elongate leaf cells; smooth, reddish setae; inclined, oval capsules; and a hookeriaceous-type peristome. *Hookeria pallidifolia* was transferred to *Hookeriopsis* s.l. (*Brymela* Crosby & B. H. Allen, *Thamniopsis*, and *Trachyxiphium* W. R. Buck) by Geheeb and Herzog (1910) and to *Lepidopilidium* by Vaz-Imbassahy and Costa (2009). However, the species belongs in *Hookeriopsis* s. str. as evident by a few critical characters. First, the stems of *H. pallidifolia* lack a developed hyalodermis in cross-section. Although *Brymela*, *Hookeriopsis* s. str., and *Trachyxiphium* also lack a stem hyalodermis, both *Lepidopilidium* and *Thamniopsis* have a moderately to well-developed hyalodermis. Next, the leaf margins of *H. pallidifolia* are entire to crenulate. While the leaf margins of both *Thamniopsis* and *Trachyxiphium* bear swollen, often bifid teeth, those of *Brymela*, *Hookeriopsis* s. str., and *Lepidopilidium* are mostly simple or have entire margins. Furthermore, unlike the prominent costae found in *Brymela* and *Lepidopilidium*, the costae in *Hookeriopsis* s. str. are short, weakly prominent, terminate below the middle of the leaf, and do not project at the tips. Lastly, the stomata of *H. pallidifolia* are rudimentary with four or five subsidiary cells, unlike those of *Lepidopilidium*, which only have two subsidiary cells.

Some confusion surrounds the distribution of *Hookeriopsis pallidifolia* based on the specimen cited in Mitten's (1875) protologue. Dickson obtained his East Indies specimen from a returning trade vessel that likely noted only the last destination in its voyage. According to Mitten (1875: 360), Dickson's East Indies specimens are likely to have been collected on St. Helena Island.

Hookeriopsis crispifolia (W. R. Buck & M. Wigginton) J. J. Atwood, comb. nov. Basionym: *Lepidopilidium crispifolium* W. R. Buck & M. Wigginton, in Wigginton & Buck, J. Bryol. 35: 270. 2013. TYPE CITATION: St. Helena. Diana's Peak National Park, compartment Actaeo 09, wet rocks by stream in deep valley, shaded under ferns, growing with *Riccardia* Gray sp. and *Fissidens elegans* Brid., 744 m, 30L/TH/107323, 5°42′W, 15°58′S, 25 Oct. 2005, *Wigginton 05/237*. TYPE: [United Kingdom, overseas territory.] St. Helena. Diana's Peak Natl. Park, Cuckold's Peak, Actaeo 09, wet rocks by stream, shaded under ferns in deep valley; with *Riccardia* spp. and *Fissidens elegans*, 744 m, 30L/TH/107323, 5°42′W, 15°58′S, 25 Oct. 2005, *Wigginton 05/237* (holotype, E not seen; isotype, NY!).

Lepidopilidium crispifolium was described from St. Helena Island based on specimens having strongly contorted, twisted leaves; plane leaf margins; short, double costae that are one third the leaf length; autoicous sexuality; and long, smooth setae. It also deviates from *Lepidopilidium* in a few critical characteristics. *Lepidopilidium crispifolium* lacks both

a complanate habit and a stem hyalodermis. Furthermore, the stomata are rudimentary with four or five subsidiary cells. Although *L. crispifolium* was described as lacking an annulus, a persistent annulus of two or three rows of subquadrate, differentiated cells, with one to three riblike thickenings on the inner cell walls, was found attached to an operculum in *Wigginton 05/549* (NY). This combination of characters indicates a closer relationship to *Brymela* and *Hookeriopsis* s. str. rather than *Lepidopilidium*. *Brymela* and *Hookeriopsis* s. str. differ mainly in the length of their costae: *Brymela* has thick, long costae, whereas *Hookeriopsis* s. str. has short, indistinct costae. Since *L. crispifolium* also has short, indistinct costae, it is better placed with *H. pallidifolia* in *Hookeriopsis* s. str. The two species represent the first reports of *Hookeriopsis* s. str. from outside of the Caribbean.

Thamniopsis chenagonii (Renauld & Cardot) J. J. Atwood, comb. nov. Basionym: *Lepidopilum chenagonii* Renauld & Cardot, Suppl. Prodr. Fl. Bryol. Madagascar 80. 1909. *Lepidopilidium chenagonii* (Renauld & Cardot) Renauld & Cardot, in Grandidier, Hist. Phys. Madagascar, Mousses 415. 1915. TYPE CITATION: Madagascar: Montagne d'Ambre près Diego Suarez, *Chenagon*, 1890. TYPE: Madagascar. Diego Suarez, 1890, *Chenagon s.n.* (lectotype, designated here, PC!; isotype, PC!).

Thamniopsis chenagonii is a yellowish green, slender species with weakly complanate-foliate stems and erect branches. In cross-section, the stems have a well-developed hyalodermis, two or three rows of small, thick-walled subepidermal cells, and enlarged cortical cells. The dorsal, ventral, and lateral leaves are somewhat contorted when dry, short, asymmetrical, and oblong-ovate, and have acute to broadly acuminate apices. In addition, the leaves have rhomboidal apical and median cells, swollen teeth along the upper leaf margins, and costae that extend to above the midleaf, prominently project at the tips, and are toothed along the back. The setae of *T. chenagonii* are reddish yellow, elongate (5–7 mm), flexuous, and smooth. The capsules are horizontal to pendent, short, and ovoid. The exothecial cells are collenchymatous, and the stomata are scattered on the neck, rudimentary, and composed of four subsidiary cells. The presence of the rudimentary stomata, consistently inflated marginal teeth, and costae with prominent serrations exclude this species from *Lepidopilidium*. The name is better placed in the more widely circumscribed genus *Thamniopsis*. Duplicates of the type collection are deposited at PC. The largest of these is designated as the lectotype.

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